The recovery of target locations in space across movements of eyes and head

Martin Szinte

THESE DE DOCTORAT DE L'UNIVERSITE PARIS DESCARTES
Cognition, Comportements et Conduites Humaines (ED 261)

Laboratoire Psychologie de la Perception (UMR 8158)
45 rue des Saints-Pères, 75006, Paris, France
http://www.lpp.psycho.univ-paris5.fr

The recovery of target locations in space across movements of eyes and head

Le rétablissement des positions d'un objet dans l'espace à travers des mouvements des yeux et de la tête

Martin Szinte
Pour l'obtention du grade de docteur de
l'Université Paris Descartes
en Psychologie Expérimentale

Patrick Cavanagh
Directeur de thèse

Date de la soutenance
29 octobre 2012

Membres du jury
Eli Brenner, rapporteur
Patrick Cavanagh, directeur de thèse
Heiner Deubel, rapporteur
Pascal Mamassian, examinateur
Pieter Medendorp, examinateur
Rufin VanRullen, examinateur

Résumé

Le système visuel a évolué de manière à prendre en compte les conséquences de nos mouvements sur notre perception. L'évolution nous a particulièrement doté de la capacité à percevoir notre environnement visuel comme stable et continu malgré les importants déplacements de ses projections sur nos rétines à chaque fois que nous déplaçons nos yeux, notre tête ou notre corps. Des études chez l'animal ont récemment montré que dans certaines aires corticales et sous-corticales, impliquées dans le contrôle attentionnel et dans l'élaboration des mouvements oculaires, des neurones sont capables d'anticiper les conséquences des futurs mouvements volontaires des yeux sur leurs entrées visuelles. Ces neurones prédisent ce à quoi ressemblera notre environnement visuel en re-cartographiant la position des objets d'importance à l'endroit qu'ils occuperont après l'exécution d'une saccade.

Dans une série d'études, nous avons tout d'abord démontré que cette re-cartographie pouvait être évaluée de manière non invasive chez l'Homme avec de simples cibles en mouvement apparent. En utilisant l'enregistrement des mouvements des yeux combinés à des méthodes psychophysiques, nous avons déterminé la distribution des erreurs de re-cartographie à travers le champ visuel et ainsi découvert que la compensation des saccades oculomotrices se faisait de manière relativement précise. D'autre part, les patterns d'erreurs observés soutiennent un modèle de la constance spatiale basé sur la re-cartographie de pointeurs attentionnels et excluent d'autres modèles issus de la littérature. Par la suite, en utilisant des objets en mouvement continu et l'exécution de saccades au travers de leurs trajectoires, nous avons mis à jour une visualisation directe des processus de re-cartographie. Avec ce nouveau procédé nous avons à nouveau démontré l'existence d'erreurs systématiques de correction pour les saccades, qui s'expliquent par une re-cartographie imprécise de la position attendue des objets en mouvement. Nous avons par la suite étendu notre modèle à d'autres types de mouvements du corps et notamment étudié les contributions de récepteurs sous-corticaux (otoliths et canaux semi-circulaires) dans le maintien de la constance spatiale à travers des mouvements de la tête. Contrairement à des études décrivant une compensation presque parfaite des mouvements de la tête, nous avons observé une rupture de la constance spatiale pour des mouvements de roulis mais pas pour des mouvements de translation de la tête. Enfin, nous avons testé cette re-cartographie de la position des objets compensant un déplacement oculaire avec des cibles présentées à la limite du champ visuel, une re-cartographie censée placer la position attendue de l'objet à l'extérieur du champ visuel. Nos résultats suggèrent que les aires visuelles cérébrales impliquées dans ce processus de re-cartographie construisent une représentation globale de l'espace allant au-delà du traditionnel champ visuel. Pour finir, nous avons conduit deux expériences pour déterminer le déploiement de l'attention à travers l'exécution de saccades. Nous avons alors démontré que l'attention capturée par la présentation brève d'un stimuli est re-cartographiée à sa position spatiale correcte après l'exécution d'une saccade, et que cet effet peut être observé avant même l'initiation d'une saccade.

L'ensemble de ces résultats démontre le rôle des pointeurs attentionnels dans la gestion du rétablissement des positions d'un objet dans l'espace ainsi que l'apport des mesures comportementales à un champ de recherche initialement restreint à l'électrophysiologie.

Abstract

The visual system has evolved to deal with the consequences of our own movements on our perception. In particular, evolution has given us the ability to perceive our visual world as stable and continuous despite large shift of the image on our retinas when we move our eyes, head or body. Animal studies have recently shown that in some cortical and sub-cortical areas involved in attention and saccade control, neurons are able to anticipate the consequences of voluntary eye movements on their visual input. These neurons predict how the world will look like after a saccade by remapping the location of each attended object to the place it will occupy following a saccade.

In a series of studies, we first showed that remapping could be evaluated in a non-invasive fashion in human with simple apparent motion targets. Using eye movement recordings and psychophysical methods, we evaluated the distribution of remapping errors across the visual field and found that saccade compensation was fairly accurate. The pattern of errors observed support a model of space constancy based on a remapping of attention pointers and excluded other known models. Then using targets that moved continuously while a saccade was made across the motion path, we were able to directly visualize the remapping processes. With this novel method we demonstrated again the existence of systematic errors of correction for the saccade, best explained by an inaccurate remapping of expected moving target locations. We then extended our model to other body movements, and studied the contribution of sub-cortical receptors (otoliths and semi-circular canals) in the maintenance of space constancy across head movements. Contrary to studies reporting almost perfect compensations for head movements, we observed breakdowns of space constancy for head tilt but not head translation. Then, we tested remapping of target locations to correct for saccades at the very edge of the visual field, remapping that would place the expected target location outside the visual field. Our results suggest that *visual* areas involved in remapping construct a global representation of space extending out beyond the traditional visual field. Finally, we conducted experiments to determine the allocation of attention across saccades. We demonstrated that the attention captured by a brief transient was remapped to the correct spatial location after the eye movement and that this shift can be observed even before the saccade.

Taken together these results demonstrate the management of attention pointers to the recovery of target locations in space as well as the ability of behavioral measurements to address a topic pioneered by eletrophysiologists.

Table of contents

1. Acknowledgements

Above all, I would like to thank Patrick Cavanagh. For the last four years, Patrick offered me what anyone doing a thesis would expect from a supervisor, and even more.
Patrick has given me invaluable help with preparing and writing my thesis and the articles it contains. He took an unimaginable time reviewing my papers, my analysis, my figures and so on, giving me consistently enlightening comments and suggestions, as if he were never too tired to read and rephrase again and again my ideas and my terribly formed English sentences.

Moreover, from the first day in his team, he has supported my work and projects. In between other things, he gave me the opportunity to do a thesis under his supervision, send me around the world to international conferences, present my work at uncountable workshops he organized, and now even help me with my post-doctoral projects. I hope I was able to take even a glimpse of his intelligence, which would be sufficient for a long scientific career.

Next, I would like to thank my laboratory and all the people it is comprised of, particularly the current and former members of the CAVlab as well as Marisa Carrasco and her people in New York University. I thank particularly Martin Rolfs who taught me all I know on eye movement analysis and John Greenwood who agreed to revise the English herein.

Then, I thank my family and especially Elodie Parison who has helped me every single day since I met her. She managed to direct my focus and together with my lovely daughter Alice, are the bases of my previous and future accomplishments. I also thank my mother for her support and for her help taking care of my daughter, giving me the time to write the manuscript.

I thank the members of my jury for doing me the honor of judging my work: Eli Brenner, Heiner Deubel, Pascal Mamassian, Pieter Medendorp and Rufin VanRullen.

Finally, I acknowledge the indispensable financial support of the *Ministère de l'Enseignement supérieur et de la Recherche*, the Université Paris Descartes and the *Ecole Doctorale 26*1 directed by Nicole Fiori, as well as the *Chaire d'Excelence* and *ANR* research grant to Patrick Cavanagh.

2. Résumé en français

Nos mouvements sont principalement guidés par ce que nous voyons et, en retour, ces mouvements affectent notre perception du monde. Les mouvements de notre corps, de notre tête et de nos yeux modifient les projections visuelles sur nos rétines et de ce fait compliquent nos interactions avec les objets qui nous entourent. On notera par ailleurs que la robotique s'inspire souvent des systèmes biologiques pour résoudre les problèmes de mise en œuvre d'un guidage visuel chez des robots en mouvement. En effet, notre cerveau semble avoir évolué de manière à prendre correctement en compte les différents aspects d'une perception effectuée via des récepteurs sensoriels en mouvement.

Un des aspects de cette perception réside dans la récupération d'un monde visuel détaillé et stable malgré les changements drastiques s'opérant lors d'un mouvement rapide des yeux, aussi appelé « saccade ». En effet, bien que l'on ait l'illusion de voir un environnement visuel uniforme et détaillé, cette impression se doit de surmonter les effets de nos fréquents mouvements des yeux (près de 5 mouvements des yeux par seconde, voir Rayner, 1998). Ainsi, notre cerveau reçoit et traite des images issues de la rétine et à partir de ces données, créé une représentation stable de l'espace nous permettant, par exemple, de conduire sans accident sur des routes embouteillées, de marcher à travers des foules en mouvement ou encore de simplement jouer au tennis. Ces trois situations impliquent la répétition de rapides mouvements des yeux, du corps et de la tête. Mais comment nos cerveaux parviennent-ils à récupérer une représentation spatiale de notre environnement visuel qui soit stable et détaillée?

Ce problème a précédemment été décrit comme le problème de la « constance spatiale » et a été au cours des derniers siècles le centre d'intérêt de bon nombre de chercheurs et philosophes. Plus récemment, cette question a reçu un tout nouvel essor grâce à l'apport de nouvelles solutions théoriques au problème de la constance spatiale issues des travaux de différents physiologistes.

Ainsi, plusieurs décennies de recherche ont permis de démontrer que notre cerveau contient de nombreuses aires visuelles dans lesquelles des cellules individuelles traitent une part limitée du champ visuel. Chaque cellule voit alors le monde à travers une fenêtre de taille réduite, une fenêtre qu'on appelle « champ récepteur » (Barlow, 1953; Daniel & Whitteridge, 1961; Hubel & Wiesel, 1962), tant et si bien que toutes ces cellules combinées ensemble définissent des cartes des images se projetant sur la rétine. Suite à l'émergence des techniques d'enregistrements simultanés chez le singe éveillé de l'activité unitaire des cellules visuelles et des mouvements des yeux (Robinson, 1963, 1964), il a été démontré que certains neurones parviennent à anticiper ce qui va se retrouver dans leur champ récepteur une fois la saccade effectuée (Duhamel, Colby & Goldberg, 1992; Gnadt & Andersen, 1988; Goldberg & Bruce, 1990). Ces neurones sont localisés dans des aires cérébrales corticales et sous-corticales telles que l'aire intra-pariétale inférieure (LIP), frontal eye fields (FEF), ou le colliculus supérieur (SC). Ces aires sont impliquées dans la coordination visuo-motrice tout en étant largement engagées dans des processus d'attention visuelle spatiale. Contrairement aux cellules visuelles normales qui traitent différentes informations uniquement dans leurs champs visuels, ces neurones en se basant sur les coordonnées d'un futur mouvement des yeux (en utilisant une copie efférente

de la commande motrice, Sommer & Wurtz, 2002; Sperry, 1950; von Holst & Mittelstaedt, 1950) « re-cartographient » leurs champs récepteurs et ainsi prédisent ce à quoi le monde visuel ressemblera après la saccade. Cette re-cartographie peut donc être vue comme un transfert d'informations entre deux cellules sur des cartes de la rétine (ou carte rétinotopique) permettant la poursuite d'un objet d'intérêt à travers un mouvement des yeux et ainsi potentiellement le maintien de la constance spatiale (voir Figure 1).

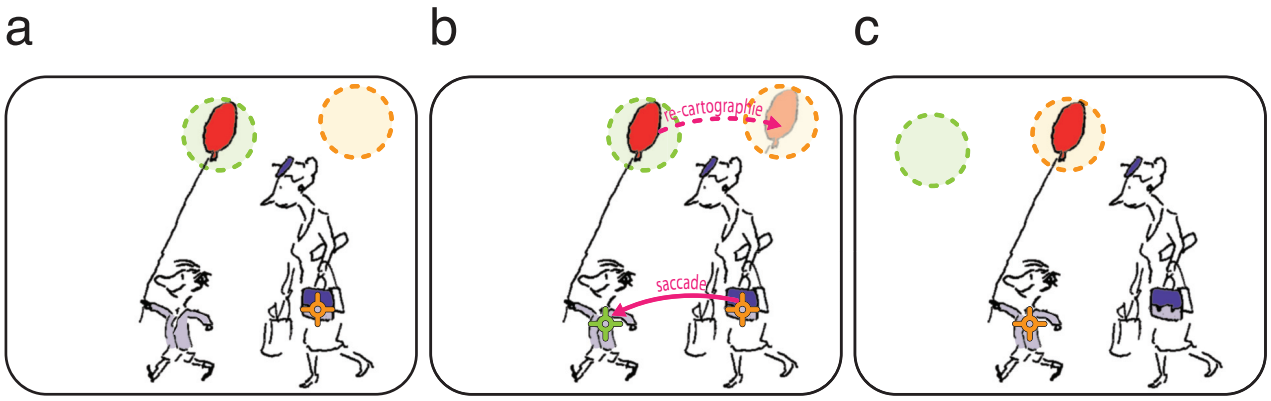


Figure 1. Re-cartographie. (a) En fixant le sac tenu par la femme (croix orange), différentes cellules visuelles traitent l'image à travers des fenêtres de vision limitées (cercles en pointillé orange et vert). Ces fenêtres définissent des positions relatives par rapport au point de fixation et se déplacent avec les yeux. (b) Avant l'exécution d'une saccade (flèche magenta) allant du sac (croix orange) à la chemise du petit garçon (croix verte), l'activité d'une cellule visuelle traitant le ballon du petit garçon (cercle pointillé vert) est transférée dans la direction opposé à la saccade (flèche magenta en pointillé). (c) Les cellules prévoient alors que le ballon apparaîtra dans le champ récepteur qui traitera cette position après la saccade (le cercle pointillé orange), permettant ainsi la poursuite de la position du ballon dans l'espace malgré les changements de coordonnées sur la rétine du fait de la saccade.

Bien qu'au niveau simplifié de deux cellules échangeant leurs informations dans le cas d'une simple saccade, le problème de la constance spatiale semble simple à résoudre, notre vision dépend de plusieurs milliers de cellules rendant le mécanisme plus compliqué à mettre en place. De plus, il n'est pas à ce jour évident que le fait de prédire qu'une saccade va apporter un stimulus à l'intérieur d'un certain champ récepteur permette réellement la poursuite attentionnelle de cet objet à travers le mouvement des yeux. D'autre part, aucune étude à ce jour n'affirme que cette mise à jour des positions rétinotopiques via une re-cartographie permette l'élaboration de la constance spatiale. Ainsi, le mécanisme de re-cartographie apporte certainement une contribution importante à la solution du problème de la constance spatiale mais rien n'indique qu'il permette de le résoudre (voir Wurtz, 2008, pour une revue de questions).

Autrement que chez le singe, la constance spatiale chez l'homme a aussi été au centre de bon nombre d'expériences. Ainsi René Descartes (voir Bridgeman, 2007) a sans doute été le premier à remarquer que le fait de taper sur le bord des yeux déplace notre perception du monde de manière systématique, alors qu'un déplacement volontaire des yeux d'une amplitude similaire n'a aucune conséquence sur sa stabilité. En effet, appuyer sur le globe oculaire entraîne soudainement à voir les objets nous entourant se déplacer. Ce soudain déplacement correspond alors aux conséquences attendues d'un mouvement des yeux si la perception ne reflétait qu'une simple lecture, sans autre traitement, des entrées visuelles.

Suivant cette observation mais aussi l'idée que notre perception trans-saccadique dépend d'un « effort de volonté » (von Helmholtz, 1867), des psychologues développèrent de nombreux protocoles expérimentaux impliquant le déplacement des mouvements des yeux. Leurs expériences inspectèrent des aspects tels que l'absence de perception du flou inhérent aux rapides déplacements des yeux, tel que l'invisibilité des déplacements d'image pendant la saccade, tel que les capacités de mémoire des caractéristiques visuelles à travers la saccade, ou encore la précision des processus de compensation lors de l'élaboration de plusieurs mouvements oculaires. D'autres études portèrent alors sur la distorsion de la localisation des objets flashés brièvement à proximité temporelle et spatiale d'une saccade ou encore sur les processus d'adaptation et de perception de phénomène visuel dans un cadre de référence spatiale. L'ensemble de ces études présente une variété d'effet et d'interprétation des mécanismes sous-tendant la constance spatiale, une variété parfois difficile, voir impossible, à intégrer avec les récents résultats issus de l'électrophysiologie chez l'animal.

L'objectif principal de cette thèse est donc d'intégrer autant qu'il se peut les résultats issus de l'électrophysiologie et de la psychologie de la constance spatiale en utilisant un autre aspect de la vision à travers le mouvement des yeux et de la tête : l'attention visuelle.

L'attention visuelle se définie en neurosciences comme une modulation de l'activité des neurones favorisant l'information pertinente du flux de données parvenant à nos yeux (Treue, 2003). L'attention, en effet, joue un rôle majeur dans les expériences de re-cartographie physiologique, ainsi que pour la constance spatiale. Entre autre, la re-cartographie des champs récepteurs ne s'observe pas si l'objet à re-cartographier n'attire pas l'attention visuelle (Gottlieb, Kusunoki, & Goldberg, 1998 ; Kusunoki, Gottlieb, & Goldberg, 2000). Aussi, l'attention visuelle et le contrôle moteur des yeux et de la tête partagent de nombreuses aires corticales et sous-corticales (Awh, Armstrong, & Moore, 2006 ; Moore, 2006).

Nous proposons donc que la constance spatiale s'explique par le déploiement de pointeurs attentionnels en prévision du déplacement des yeux. Ces pointeurs attentionnels sous-tendent ainsi la constance spatiale aux différents niveaux de l'analyse visuelle, joignant ensemble à travers les saccades les différentes caractéristiques visuelles (la forme, la couleur, l'orientation) d'objets attirant notre attention (Cavanagh, Hunt, Afraz & Rolfs, 2010).

Dans cette thèse nous proposons tout d'abord une revue de question sur des différents résultats issus de travaux en psychophysique et en électrophysiologie sur le thème de la constance spatiale lors d'un déplacement des yeux ou de la tête. Nous concluons alors cette revue de question par la présentation de notre modèle de maintien de la constance spatiale par la re-cartographie de pointeurs attentionnels avant de présenter une série d'études empiriques visant à tester le modèle et à démontrer l'optimalité de l'étude des processus attentionnels pour évaluer la re-cartographie chez l'homme.

Dans cette série d'études, nous avons tout d'abord démontré que cette re-cartographie pouvait être évaluée de manière non invasive chez l'Homme avec de simples cibles en mouvement apparent

(voir article : *Spatiotopic apparent motion reveals local variation in space constancy*). En utilisant l'enregistrement des mouvements des yeux combinés à des méthodes psychophysiques, nous avons déterminé la distribution des erreurs de re-cartographie à travers le champ visuel et ainsi découvert que la compensation des saccades oculomotrices se faisait de manière relativement précise. D'autre part, les patterns d'erreurs observés soutiennent que la constance spatiale est basée sur la re-cartographie de pointeurs attentionnels et excluent d'autres modèles issus de la littérature.

Par la suite, en utilisant des objets en mouvement continu et l'exécution de saccades au travers de leurs trajectoires, nous avons mis à jour une visualisation directe des processus de re-cartographie (voir article : *Temporal dynamics of remapping captured by peri-saccadic continuous motion*). Avec ce nouveau procédé, nous avons à nouveau démontré l'existence d'erreurs systématiques de correction pour les saccades, qui s'expliquent par une re-cartographie imprécise de la position attendue des objets en mouvement.

Nous avons par la suite étendu notre modèle à d'autres types de mouvements du corps et notamment étudié les contributions de récepteurs vestibulaires sous-corticaux (otoliths et canaux semi-circulaires) dans le maintien de la constance spatiale à travers des mouvements de la tête (voir artilce : *Visual space constancy across head roll and head translation*). Contrairement à des études décrivant une compensation presque parfaite des mouvements de la tête, nous avons observé une rupture de la constance spatiale pour des mouvements de roulis mais pas pour des mouvements de translation de la tête.

Ensuite, nous avons testé cette re-cartographie de la position des objets compensant un déplacement oculaire avec des cibles présentées à la limite du champ visuel, pour une re-cartographie censée placer la position attendue de l'objet à l'extérieur du champ visuel (voir article : *Apparent motion from outside the visual field, retinotopic cortices may register extra-retinal positions*). Nos résultats suggèrent que les aires visuelles cérébrales impliquées dans ce processus de re-cartographie construisent une représentation globale de l'espace allant au-delà du traditionnel champ visuel.

Pour finir, nous avons conduit deux expériences pour déterminer le déploiement de l'attention à travers l'exécution de saccades (voir article : *Allocation of attention across saccades*). Nous avons alors démontré que l'attention capturée par la présentation brève d'un stimuli est re-cartographiée à sa position spatiale correcte après l'exécution d'une saccade, et que cet effet peut être observé avant même l'initiation d'une saccade.

L'ensemble de ces résultats démontre le rôle des pointeurs attentionnels dans la gestion du rétablissement des positions d'un objet dans l'espace ainsi que l'apport de mesures comportementales de processus attentionnels pour l'étude de la re-cartographie observé initialement dans des travaux d'électrophysiologie.

3. Introduction

3.1 Prologue

Our movements are predominantly guided by what we see and, in return, these movements affect our perception of the world. Movements of our body, head and eyes modify the visual projections on our retinas and thus complicate our interactions with both static and moving objects. Interestingly, when scientists attempt to implement visual guidance in mobile robots, they often look to biological systems for answers as our brains evolved in order to deal with all aspects of the challenges that arise with perception using moving sensors.

One of these challenges relies on the recovery of a detailed stable world despite the drastic changes due to rapid eye movements, also called “saccades“. Indeed, although one might have the illusion of seeing a uniformly detailed visual world, this impression must overcome the effects of the frequent (up to five times per second, see Rayner, 1998) displacements of our eyes (see Figure 1). The brain receives and treats images from the retina and uses these inputs to create a stable representation of space allowing us to, for example, efficiently drive along congested roadways, walk on crowded sidewalks or simply play tennis, three common situations implying repetition of rapid eye body and head movements. How does our brain recover this stable and detailed spatial representation of the visual scene?

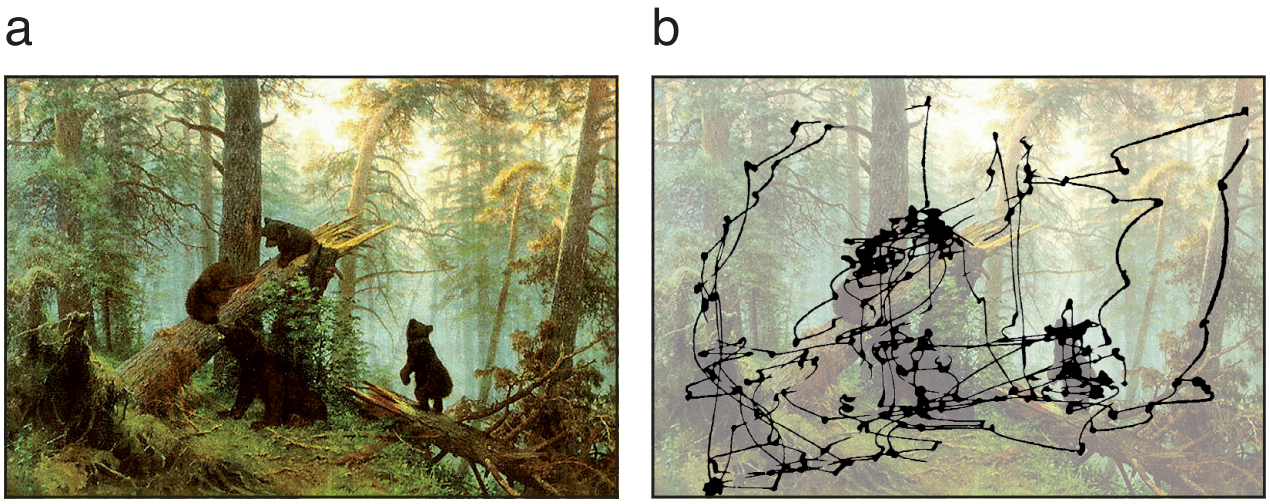


Figure 1. Historical oculomotor recordings from Alfred L. Yarbus (1967). (a) Landscape painting executed by Ivan I. Shishkin in 1889, entitled “*Morning in the pine forest*”, today displayed in the Tretyakov Gallery of Moscow, Russia. (b). Oculomotor eye traces in a free viewing of the painting, line and back dots show saccades and fixation periods, respectively. These traces were collected in a 2-minute free examination of the painting and illustrate well both the frequency of the saccade as well as the rapid succession of fixation and saccade periods.

This problem is described in the literature as the “space constancy” problem and has been a matter of debate and interest for centuries. More recently this question has received a revival of interest when physiologists brought new perspectives to the existing theoretical solutions of the space constancy problem.

Interestingly, decades of research have demonstrated that our brain contains numerous visual areas where individual cells treat a limited part of the visual field. Each cell sees the world through a

restricted window called a “receptive field” (Barlow, 1953; Daniel & Whitteridge, 1961; Hubel & Wiesel, 1962). These restricted views must be combined together to define maps of the image that has fallen on the retina. Following the rise of simultaneous single cell and eye movement recordings in awake monkeys (Robinson, 1963, 1964), it has been shown that some neurons briefly shift the location of their receptive field so that they begin responding to a target that will fall in their receptive field after the completion of a saccade – even before it does so (Duhamel, Colby, & Goldberg, 1992; Gnadt & Andersen, 1988; Goldberg & Bruce, 1990). This process, called “remapping”, is seen in neurons that are located in cortical and sub-cortical areas such as the lateral intraparietal area (LIP), the frontal eye fields (FEF) and the superior colliculus (SC). These areas are involved in visuo-motor coordination of both the head and the eyes and are strongly engaged in visual attention processing. These neurons “remap” their receptive field using information about where the eye will move (i.e. the efference copy of a motor command that will drive the eye movement, Sommer & Wurtz, 2002; Sperry, 1950; von Holst & Mittelstaedt, 1950) and therefore predict what the world will look like following a saccade. This “remapping” can be seen as a transfer of information between two cells (the one normally responding to the target and the one that will respond to it after the saccade) on a “retinotopic” map (i.e. a map of the retina) to keep track of an object of interest and maintain the illusion of a stable world across saccade (see Figure 2).

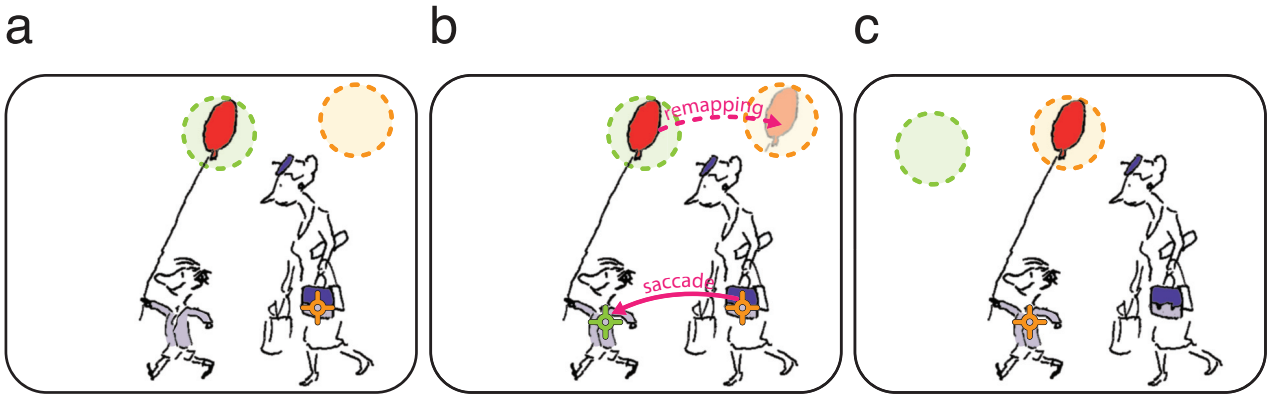


Figure 2. Remapping. (a) When fixating the woman’s purse (orange cross), different visual cells see the image through limited windows (orange and green dashed circles). These windows define positions relative to the point of fixation and move with the eyes. (b) Before the execution of a saccade (magenta arrow) going from the purse (orange cross) to the boy’s shirt (green cross), the activity of the visual cell processing the boy’s balloon (green circle) is transferred in the opposite direction of the saccade (dashed magenta arrow). (c) The balloon is then expected to fall in the window that will process its location after the saccade (the orange circle), keeping track of the locations of targets in the world despite the effects of eye movements on the retinal image.

Although the space constancy problem seems easy to solve at the simplified level of two cells with one unique saccade, our vision relies on thousands of these cells. This makes the constancy process a complicated one to implement. In theory, the ability to predict when a saccade will bring stimuli inside the receptive field should help us to keep track of stimuli of interest. However, it is not clear, and no study has yet affirmed that this updating through remapping provides space constancy. It certainly has the potential to make an important contribution, but we do not yet know whether that is all there is to solve (see Wurtz, 2008, for a review).

Space constancy has also been the focus of many experiments in humans. René Descartes (see Bridgeman, 2007), a pioneer philosopher and psychologist, was perhaps the first to point out that while tapping on the eye systematically moves the world, no such instability is seen when we make eye movements of similar amplitude. Indeed, the effect we see when we push mechanically on our eyeball gives us the impression that fixated visual objects surrounding us suddenly start to jiggle, acting as one might imagine they should if our perception simply reflected the output of our retinas.

Following on from this observation, as well as the idea that trans-saccadic perception relies on an effort of will (von Helmholtz, 1867), psychologists developed several movement-contingent protocols to explore different aspects of perception when the eyes, head and body are in motion. Their experiments examined the absence of the inherent blur that should be seen when our eyes move, as well as the invisibility of large image shifts during saccades (saccadic suppression), the memory and capacity our visual system to retain features across saccades (trans-saccadic memory and trans-saccadic integration), the accuracy of the compensation processes occurring with several serial eye movements (e.g., double step saccade tasks), the localization distortions occurring in the vicinity of a saccade (peri-saccadic mislocalization and compression) and the perception and adaptation processes occurring in a spatiotopic reference frame. Overall, these studies present a variety of interpretations of space constancy mechanisms that are sometimes hard to reconcile with the physiology of remapping mentioned above.

The central purpose of this thesis is to integrate, as much as possible, the evidence of physiology and psychology of one central aspect of space constancy: remapping, the correction of target location for the effects of eye and head movements. We will propose that visual attention is the mechanism underlying these corrections.

Visual attention is defined in neuroscience as a modulation of cells' activity favoring task-relevant information from the stream of data entering our eyes (Treue, 2003). Attention has played a major role in "remapping" experiments involving space constancy. First, the receptive field remapping is not found if the visual object to be remapped is not attended (Gottlieb, Kusunoki, & Goldberg, 1998; Kusunoki, Gottlieb, & Goldberg, 2000). Second, visual attention and the control for eye and head movements share several cortical and sub-cortical networks (Awh, Armstrong, & Moore, 2006; Moore, 2006).

We propose to explain the remapping aspect of space constancy as a re-allocation of attention "pointers" (which can be seen as spotlights on parts of the visual field) at the time of a saccade. Attention pointers then tie together the visual features (shape, color, orientation, etc.) of an attended object as well as its location across saccades (Cavanagh, Hunt, Afraz, & Rolfs, 2010).

We first show that this attentional remapping could be evaluated in a non-invasive fashion in humans with simple apparent motion targets (Szinte & Cavanagh, 2011). Using eye movement recordings and psychophysical methods, we evaluated the distribution of remapping errors across

the visual field and determined which models of space constancy best fit with the pattern observed. In a second study, using targets that moved continuously while a saccade was made across the motion path, we directly visualized remapping processes as they occurred, a method that allowed us to determine some of its temporal as well as spatial characteristics (Szinte, Wexler, & Cavanagh, 2012). We then extended our model to other body movements, and studied the contribution of sub-cortical receptors (the otoliths and the semi-circular canals) in the maintenance of target location across head movements. Contrary to studies reporting accurate compensation for head movements, we observed serious breakdowns of space constancy for head tilt but not for head translation. In a fourth study, we tested the limits of attentional remapping for a target presented at the very edge of the visual field. We showed that remapping could take place at target locations falling outside the visual field. Then, in a final study, we determined the allocation of attention across saccades in order to demonstrate that the attention captured by a brief transient was remapped to the correct spatial location after the eye movement and that this shift can be observed even before the saccade.

These studies question and test the limits of previously reported models of space constancy, as well as our model of the recovery of target locations in space across eye and head movements through the remapping of attention pointers.

3.2 The problem of space constancy

3.2.1. Space constancy, a constant updating of internal representations of location

As discussed above, our visual perception does not simply reflect the output of our eyes. Visual perception relies on active processes modifying, altering and generally optimizing the treatment of our visual environment (Findlay & Gilchrist, 2003). These modifications put us in the optimal condition to properly and quickly interact with everything from the most simple to the most complex visual environments that we may encounter.

Indeed, our binocular visual fields cover 200 to 220 degrees of visual angle (Harrington, 1981) and although we experience the perception of a fully and uniformly detailed visual world, the retinal surface where the photoreceptors lie is far from uniform. As with several other predators, evolution has endowed us with a small pit on the retinal surface, no bigger than 1.5 mm, corresponding to the area of high acuity. This region, named the *fovea,* concentrates the highest proportion of the photoreceptors responsible for detailed vision, the cones (Hirsch & Curcio, 1989). Such a localized specialization comes with the cost that we must perform eye and head movements to keep this region of high acuity on objects of interest.

A first set of movements, the vestibulo-occular reflexes (rotational or translational) and optokinetic reflexes, is responsible for maintaining the fovea on a target object whenever we move our head or body. These eye movements rely on information from the vestibular system and from patterns of coherent optic flow on the retina (Leigh & Zee, 1999). In contrast with these reflexive movements, voluntary eye movements deal with a selected target in a number of ways. The pursuit system maintains the foveation of moving objects; the vergence system governs foveation in depth and, of special interest for the topic of space constancy, the saccadic system translates the eyes in two dimensions at very high velocities across large distances to bring a target of interest onto the fovea (Leigh & Zee, 1999). Finally, adding some complexity to our visual system, we can also rotate our head in three different directions (yaw, roll and pitch), and translate the head on its own or together with the whole body in the three lateral dimensions.

With the exception of reflexive eye movements, all these movements modify the projections of the visual world falling on the retina. However, despite these retinal projection changes, we seldom incorrectly interpret motion on the retina caused by an eye movement as a displacement of a stable object, nor does an eye movement cancel the impression of the motion of a moving object so that it is seen as stable.

The first question addressed by this thesis is how a stable, detailed and continuous visual world emerges from the frequently moving images with non-uniform resolution that our light sensitive receptors send to the visual brain. A second more specific question is how we recover the position of objects in the world across shifts of the eyes and head.

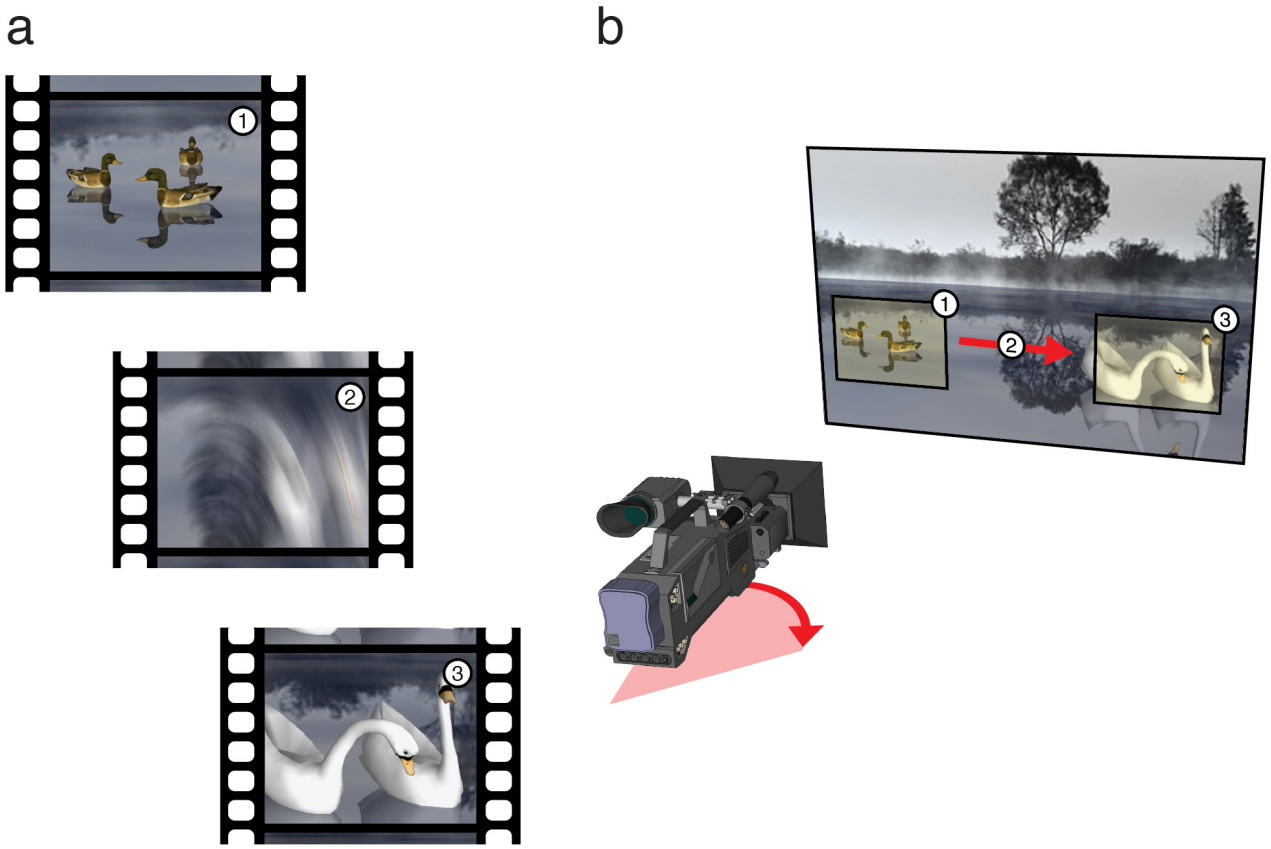


Figure 3. Visual space constancy. (a) When watching images acquired before (1), during (2) and after (3) a rapid rotation of a video camera (b) aimed at a pond scene, one sees two static images each centered on the ducks and swans with no impression of their relative locations, and a blur corresponding to the camera motion between them. We also keep "filming" as we move our eyes; however, we never see the blur and we do not experience the ducks and swans as sharing the same location. The visual system has evolved to deal with these inputs giving us the ability to properly locate objects across self-movement due to either eye, head or body movement.

To illustrate these questions, one can imagine a person seeing different images displayed on a screen, filmed from a camera moving very rapidly from left to right (see Figure 3). The moving camera captures a scene composed of ducks and swans located respectively at the left and right edges of a pond. Between the first static view of the ducks and the second of the swans, the image will blur as the camera sweeps across the pond. We also keep "filming" as our eyes or head move but we do not experience the blur and rather see only two views, one before and one after the movement. Furthermore, unlike the camera images on the screen we do not experience the ducks and swans at the same location, but rather as located at two ends of the pond, as they actually are.

Knowing that visual areas are coded in a retinotopic reference frame (Ben Hamed, Duhamel, Bremmer, & Graf, 2001; Gardner, Merriam, Movshon, & Heeger, 2008; Sereno et al., 1995; Sommer & Wurtz, 2000), perceptual stability may be understood as an updating of this retinotopic internal representation rather than a spatiotopic construction of the external world (Hall & Colby, 2011).

3.2.2. Retinal and extra-retinal signals for space constancy

Space constancy implies the active construction of a model of the visual world in order to efficiently interact with it. But what are the different cues available to achieve such construction?

Three different kinds of signals could provide information regarding world stability: retinal signals, proprioceptive signals and the efference copy of the motor command.

3.2.2.1 Retinal signals

James J. Gibson (1950, 1966) proposed that all the information one needs to see the world as stable is contained in the retinal input. He speculated that the patterns of light reaching the eyes could be thought of as an optic array containing all the visual information available to provide an unambiguous signal about the layout of objects in space. Because the world is generally stable, any motion of the entire image should be considered as arising from an eye movement rather than a displacement of the world. Although this source of information seems limited, optic flow is used by the optokinetic system to compensate for low frequency body translation (Miles, 1995). In a study comparing visual localization and pointing in illuminated and dark environments with partially curare-paralyzed observers (Matin et al., 1982), it has also been suggested that the structure of the visual environment might be sufficient to efficiently locate objects. Moreover, in a cluttered scene, the retinal motion of the most distant structure could be used to estimate eye-head rotation (together with extra-retinal signals, Brenner & van den Berg, 1996), and more recently some authors suggested that the use of optic flow could be sufficient to maintain target location on a egocentric map of space (Wolbers, Hegarty, Buchel, & Loomis, 2008).

3.2.2.2 Proprioceptive signals

The problem of space constancy could be simplified into a process of matching the past and present images that fall on the eye. As demonstrated by Sherrington (1918) the extra-ocular muscles contain stretch receptors that signal eye position in the orbit and thus may provide the necessary information to make the correspondence between the images before and after the eye movement. This theory, frequently referred to as the “inflow” theory (in opposition to the “outflow” theory described in the following paragraph), finds some support in studies measuring the error in the localization of visual objects seen when either passively moving one eye with a suction contact lens (Gauthier, Nommay, & Vercher, 1990), or when pressing on one eye currently occluded (Bridgeman & Stark, 1991). These authors found, for the particular case of maintaining fixation, that the assessment of the direction of a target depends in part on information received from proprioceptors, a part that Bridgeman & Stark (1991) evaluated as being responsible for a quarter of the compensation observed. However, this conclusion has been challenged by physiological results (see below).

Other studies have investigated head or body movements, to evaluate the contribution of other proprioceptive inputs, and found that the addition of neck proprioception or of podokinesthesic

information (proprioception of the legs) improve the capacity to saccade to or to judge the location of an object presented before a passive displacement (Jürgens & Becker, 2006; Mergner, Nasios, & Anastasopoulos, 1998; Mergner, Nasios, Maurer, & Becker, 2001).

In the critical tests of saccades, monkeys were asked to prepare a sequence of two saccades while an electrical stimulation in a different portion of the brain modified the execution of the first saccade. These studies evaluated the monkey's ability to correctly foveate the second target despite the electrical perturbation occurring before the execution of the first saccade. Updating was found to be accurate despite a stimulation delivered to the superior colliculus (Mays & Sparks, 1980; Schiller & Sandell, 1983; Sparks & Mays, 1983), to the dorsomedial frontal cortex (a structure innervating the brain stem), or to the frontal eye fields (Schiller & Sandell, 1983; Tehovnik & Sommer, 1996). Nevertheless, compensation did not occur when the eyes where moved by stimulating the motor neurons (Schiller & Sandell, 1983; Sparks & Mays, 1983).

These results, together with the accurate compensation found when the proprioceptive afferents of the eye were simply cut (Guthrie, Porter, & Sparks, 1983), suggest that proprioception could not have conveyed sufficient information about the new eye position and that in the case, for example, of stimulation of the superior colliculus or frontal eye fields, other signals might have conveyed the necessary information to correctly perform these double-step saccade tasks (Hallett & Lightstone, 1976a, 1976b).

3.2.2.3 Efference copy of the motor command

As described above, contrary to an electric perturbation of the saccade at the level of the motor neuron, the effects of stimulation in saccade areas are compensated when subsequent eye movements are executed (Guthrie et al., 1983). Such compensation is thought to originate from a copy of the motor command, the rationale being that the motor system sends a copy of the movement vector to subtract the consequence of its own movement from the sensory system.

This notion was first proposed based on the report of continually circling flight of the *Eristatlis* blowfly following a surgically imposed 180 degrees head rotation ("*efference copy*" theory, von Holst & Mittelstaedt, 1950) and from similar observations following the surgical eye inversion of a fish ("*corollary discharge*" theory, Sperry, 1950). The theory of efference copy received empirical support from physiological studies, where neural pathways and neural mechanisms were demonstrated, for example, in the electrosensory system of the *mormyrid fish*, a fish that generates electric discharge to communicate with conspecifics as well as to detect nearby danger (Bell, 1981; Poulet & Hedwig, 2007) and for the male *Grillus bimacullatus*, a cricket able to sing at sound levels superior to 100 dB SPL without going deaf, even if at that level, its auditory neurons would be desensitized if the sound had not been generated by the cricket itself (Poulet & Hedwig, 2003, 2006).

In relation to the space constancy problem, the idea that efference copy could be the determining signal, described as the outflow theory, was first elaborated by von Helmholtz who spoke about an "effort of will" (1867). His theory later received more empirical support in an extraordinary experiment by Stevens and collaborators (Stevens et al., 1976). The author self-administered a sub-paralytic dose of curare and a paralytic dose of succinylcholine (neuromuscular blocking agent) and then

attempted to move their eyes. They reported that with this sub-paralytic dose, which limited the size of their saccades but supposedly kept intact the neural outflow or efference copy, they experienced a displacement of the whole visual world in the direction of the saccade. In contrast, with a paralytic dose, “jumping” completely stopped as well as the saccades themselves.

This jumping percept fits with the idea that efference copy is taken into account for localizing objects. Specifically, the transient made by the small saccade in the sub-paralytic experiment forced the visual system to use the efference copy for the intended saccade, generating inconsistencies with the smaller executed saccade and so producing a breakdown of space constancy (Bridgeman, Van der Heijden, & Velichkovsky, 1994).

Another report supports the importance of the efference copy signal for space constancy with the simple observation that the world appears to shift when the eye is passively moved. This perceived motion was initially thought to result from the movement of the retinal image occurring without any corresponding efference copy. However, it was later proven to be due to an inconsistency between the attempt to counter the push on the eye (and thus the efference copy of such an attempt) and the absence of change in fixation position (Bridgeman & Stark, 1991; Stark & Bridgeman, 1983).

Finally, as explained previously, some of the corrections for upcoming eye movements can be detected even before the saccade begins and thus could only be the consequence of a predictive process such as efference copy. Efference copy is thus a very likely candidate for driving space constancy and, as described in the following section, it has been an active focus of physiological research in the last 20 years.

3.3 Space constancy for saccadic eye movements

3.3.1. Possible mechanisms of space constancy

Taking advantage of one of the several retinal and extra-retinal signals described in the preceding section, different mechanisms of space constancy have been described in the literature of saccadic eye movements. These mechanisms, which we will summarize in the following paragraphs, are all based on empirical results in psychophysics, electrophysiology and functional imaging. We have classified all of these mechanisms under two rough categories, the global- and the local-correction approaches of space constancy.

3.3.1.1 Global mechanisms of correction

By *global correction*, we mean that the decision about visual stability or the overall correction or calibration is determined and applied uniformly over the entire visual input (see Bridgeman et al., 1994 for a review). Among the possible global corrective mechanisms are:

1. *Neglecting the problem*: This first mechanism is indeed a lack of mechanism and assumes that the world is ecologically stable. Under such conditions there is no problem of space constancy since when the image is in motion the high-level representations of relations between objects

(an assertion such as “the table is to the right of the sofa”) and retinal information (optic arrays) support the conclusion that the eyes have moved (Gibson, 1950, 1966). Another version of this neglect of the space constancy problem comes from O’Regan (1992), who also believes in a high-level representation of relations between visual objects (personal communication) and asserts that the visual world is our memory, such that no content of the previous fixation should be retained, because information can be reacquired whenever an observer wants it, as long as its location is retained.

However, space constancy cannot be solely based on retinal signals, as the eye-press experiment and its perturbation of space constancy demonstrates (Bridgeman, 2007). Also, while the blur caused by slow movements might be used to recover the direction of a movement, the high amplitude and velocity of saccades makes the optic array information of less practical use (Bridgeman et al., 1994). Finally, in our view, the extraction of high-level representations of the relations between objects requires some active mechanism that can compute these representations and thus cannot be explained by an absence of mechanism.

2. *The subtraction correction*. With this mechanism, the efference copy or corollary discharge is used to predict the input on the retina following the eye or head movement (Sperry, 1950; von Holst & Mittelstaedt, 1950) and this is subtracted from the actual retinal signal. If a match to the new input is found, it is assumed that the world has been stable, otherwise it is ascertained that the world has moved. For example in the case of the *Eristalis* blowfly, von Holst and Mittelstaedt (1950, 1971) observed that with a surgically rotated head, its flight seemed normal in darkness but, in light, the fly continuously circled. They explained this behavior with a mechanism that subtracted the predicted visual input (predicted using efference copy) from the actual retinal signal if it was present. In the dark, this had no consequence as both would be featureless. However, in a normal, lighted environment, the difference of the predicted signal and the retinal signal from the inverted head increased rather than decreased with each corrective reorientation, producing the continuous circling of the fly.

   Although this simple and general process appears a plausible contributor to space constancy, it has been amended to allow for some degree of mismatch before stability is rejected, as there is quite a high threshold for detecting visual object displacements across saccades (Bridgeman, Hendry, & Stark, 1975). In addition, rapid alternation of saccades or eye presses alter the possible subtraction correction (Grüsser, Krizic, & Weiss, 1987; Ilg, Bridgeman, & Hoffmann, 1989).

3. *Spatiotopic maps*. Here, efference copy is used to transfer retinal input onto a higher order map coded in spatial coordinates (e.g. Andersen, Essick, & Siegel, 1985; Bischof & Kramer, 1968; Breitmeyer, Kropfl, & Julesz, 1982). This mechanism, also called the ‘translation solution” (Bridgeman et al., 1994), fits with our visual experience of space constancy and seems to simplify the problem. However this appealing theory implies the existence of spatiotopic maps that have failed to emerge from the recent rush of research in electrophysiology (Wurtz, 2008). Nevertheless, this mechanism has found some support with the report of some retinotopicaly

organized cells where the visual response is modulated or gated by the eye position in the orbit (Andersen et al., 1985; Andersen & Mountcastle, 1983) and of visual cells that respond to a position in space (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti & Battaglini, 1989; Galletti, Battaglini, & Fattori, 1995), even though these modulations might be attributed to a visuo-motor link rather than to perception, *per se* (Andersen, Snyder, Bradley, & Xing, 1997; Snyder, Batista, & Andersen, 1997).

Finally, recent evidence of spatiotopic adaptation (Melcher, 2005, 2007; see Melcher & Colby, 2008 for a review) and spatiotopic integration (Melcher & Morrone, 2003) has suggested the existence of such maps in humans but these results have been challenged recently (Afraz & Cavanagh, 2008; Knapen, Rolfs, & Cavanagh, 2009; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Morris et al., 2010; see Cavanagh et al., 2010 for a review).

4. *Saccade target, saccade landscape and calibration theory.* Here a memory of the saccade target and its surround plays a specific role in the maintenance of space constancy. Indeed, it has been shown that attention is drawn to the saccade target even before the saccade begins (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995) and that changes or displacements at that specific position are better detected than anywhere else when a saccade is executed (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; McConkie & Currie, 1996). Deubel and colleagues proposed that the saccade target is used to link the pre- and post-saccadic target location (Deubel, 2004; Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 2002; Koch & Deubel, 2007).

   Deubel and colleagues hypothesized that the visual system presumes that the world remains stable across a saccade. The saccade target and its surround is first selected and stored. After an eye movement brings the saccade target to the fovea, the visual system compares the fixation and its surround with the stored memory of the saccade target. Then, if the saccade target is found, its world coordinates are aligned to its pre-saccadic values and the assumption of stability is maintained, otherwise if the target is missing then visual stability is abandoned. It is then assumed that the target moved during the saccade.

   With this mechanism, there is no need for efference copy to predict where the target should be as the saccade itself serves that function. However, according to these authors, if nothing at all is found when the saccade lands, then this target reference approach is abandoned and the visual system will exceptionally use extra-retinal signals (Deubel, Schneider, & Bridgeman, 1996).

   Finally, Bridgeman (Bridgeman, 2007, 2010; Bridgeman et al., 1994) has modified this reference theory to add the idea that perception begins anew on every saccade. This change is in response to the findings of the inability to detect changes at an unattended location (Rensink, O'Regan, & Clark, 1997; Simons & Rensink, 2005). According to Bridgeman (2010), locations need to be computed again after each eye movement but there is special treatment (as described above) for the attended saccade target.

3.3.1.2 Local mechanisms of correction

As an alternative to these global approaches, electrophysiological studies have suggested a piecemeal compensation where predictive corrections, based on efference copy (Wurtz, 2008; Wurtz, McAlonan, Cavanaugh, & Berman, 2011), are applied to the representations of only a few attended items on the retinotopic maps of saccade control centers (Gottlieb et al., 1998; Kusunoki et al., 2000). This shift of activity for each target to its expected post-saccadic location, called "remapping," starts before the target lands and is seen even if the target is removed during or even before the saccade and so never lands there (Duhamel et al., 1992; Umeno & Goldberg, 2001).

The remapping process produces a crude spatiotopy for attended items (Cavanagh et al., 2010; Wurtz, 2008), and if it actually underlies the space constancy we experience, then displacements of any unattended items should not be seen (referred to as the change blindness phenomenon, Cavanaugh & Wurtz, 2004; O'Regan, Rensink, & Clark, 1999; Rensink et al., 1997). Critically, this change blindness occurs only for non-attended items (Rensink et al., 1997). The correction in this "remapping" proposal is then applied to individual attended targets, and so, unlike global correction schemes, there is no assumption that the correction be the same everywhere.

It is the same efference copy vector that drives the correction for each target, but the conversion of the vector to a shift on the roughly log polar coordinates of the saccade control maps is idiosyncratic for each location and direction. Indeed, in two models of this process (Keith & Crawford, 2008; Quaia, Optican, & Goldberg, 1998), the link between the target location and the saccade vector that predicts the post-saccadic location must be learned independently for each location and saccade.

In the following section we will present a selection of empirical studies of space constancy across saccadic eye movements. This selection will improve our understanding of the mechanism described above and the outcome of these studies will be seen to favor one mechanism over others as an explanation of space constancy.

3.3.2. Evidence from psychophysics

3.3.2.1 Saccadic suppression

With the high speed of saccades in normal viewing, the whole scene moves very rapidly on the retina. That displacement should normally produce a blur, however introspection clearly suggests that these inputs are perceptually suppressed: an effect reported as saccadic suppression (see Matin, 1974; Volkmann, 1986 for reviews). Rather than a complete suppression, the effect corresponds to an elevation of threshold for detecting visual flashes (Latour, 1962; Zuber & Stark, 1966), electrical phosphenes (Riggs, Merton, & Morton, 1974), object displacement (Bridgeman et al., 1975), or motion (Burr, Holt, Johnstone, & Ross, 1982) not only while the saccade is occurring but also within the 100 ms preceding and following the saccade. Saccadic suppression reduces the availability of

retinal signals during the saccade and constrains the space constancy problem to recovery of the position of objects in the world using only pre- and post-saccadic views.

Saccadic suppression informs us about the active processes occurring around the time of a saccade. For example it has been shown that a strong reduction of sensitivity occurs for detecting a target displacement (displacement of a third of the saccade amplitude is undetected, Bridgeman et al., 1975), however only weak threshold elevation is found for detecting small flashes (Latour, 1962; Riggs et al., 1974; Zuber & Stark, 1966). This difference was examined in two studies (Burr et al., 1982; Burr, Morrone, & Ross, 1994), which showed that the contrast threshold measured during saccades is unchanged for high spatial frequencies (e.g. details such as the small flash targets in saccadic suppression studies) compared to fixation, but is elevated for low spatial frequencies (e.g., large targets, as in saccadic suppression of displacement studies). Finally, threshold elevation was not observed for color-defined stimuli, suggesting that only the magno-cellular pathway is affected by saccadic suppression (Burr et al., 1994).

Different mechanisms have been proposed to explain saccadic suppression, one based on an efference copy or corollary discharge signal and the other based on visual masking (see Ross, Morrone, Goldberg, & Burr, 2001; Wurtz, 2008 for reviews).

Two empirical results suggest that extra-retinal signals drive saccadic suppression. First, saccades can make afterimages disappear in the dark even though the retinal signal from the afterimage is unaffected by the saccade (Kennard, Hartmann, Kraft, & Boshes, 1970); second, the effect of saccadic suppression precedes the saccade by 100 ms, suggesting that predictive signals of efference copy might be used to initiate the suppression.

On the other hand, there is strong evidence that forward and backward masking by pre- and post-saccadic images plays an important role in saccadic suppression. When stimuli are presented during a saccade but preceded and followed only by blank fields, they are seen without suppression (Castet, Jeanjean, & Masson, 2002; Castet & Masson, 2000; Deubel, Elsner, & Hauske, 1987).

Saccadic suppression, when it occurs, contributes in a minor way to space constancy by eliminating the blur and motion of the retinal image during the saccade. It plays no role in keeping track of target locations but does reduce the range of signals available to judge the movement of the eyes. Specifically, since visual input cannot be reliably acquired during the saccade, space constancy must be based on the pre- and post-saccadic images alone. There can be little or no processing of the images during saccade that Gibson thought would be a good indicator of self motion (Gibson, 1950, 1966). O'Regan's (1992) proposal of complete neglect of retinal and extra-retinal signals is indifferent to the effects saccadic suppression since the post-saccadic image can still act as the outside memory of spatial locations.

3.3.2.2 Mislocalization effects

When a brief probe is presented around the time of a saccade, there are frequently large errors in its perceived location. In particular, two types of mislocalization effects have been reported: peri-saccadic mislocalization and the peri-saccadic compression effect. These two effects occur when a probe is flashed briefly at one location just around the time that an observer prepares a saccade to another location (see Figure 4a). In the 200 ms bracketing the onset of the saccade, the flashed probe is significantly mislocalized toward the saccade target, in some cases by as much as the amplitude of the saccade. The main distinction between these effects is that for peri-saccadic mislocalization, a probe presented at any location on the screen is always seen mislocalized in the direction of the saccade before its onset and in its opposite direction after. In contrast, for peri-saccadic compression, objects are seen shifted toward the saccade target no matter where or when they are presented.

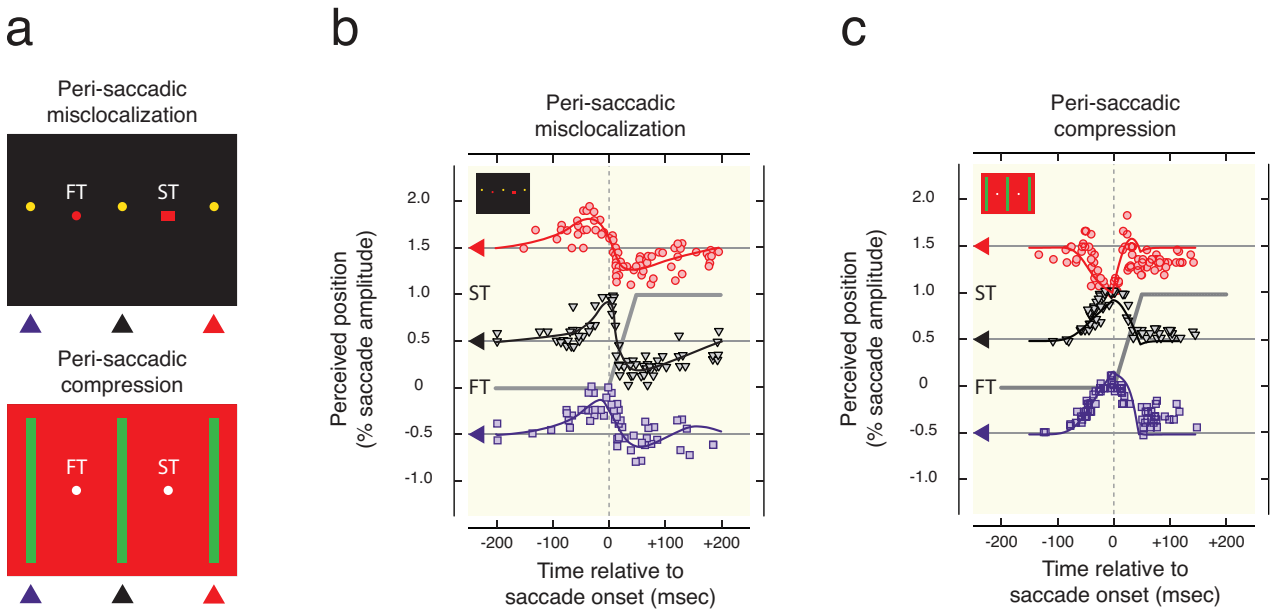


Figure 4. Peri-saccadic mislocalization and compression. (a) Stimulus configurations. To observe peri-saccadic mislocalization effects, Honda (1991) put observers in complete darkness and instructed them to saccade from the fixation (FT) to the saccade target (ST). He flashed a yellow LED (2 ms) at different times relative to the saccade onset. The flash could have different spatial locations, either in between the fixation and saccade targets (black arrow), beyond the saccade target (red arrow) or on the opposite side of the fixation target (purple arrow). Note that in Honda's experiment the saccade was vertical but has been rotated here to compare with compression paradigm. To observe peri-saccadic compression effects, Ross et.al (1997) used a similar configuration except that the display and test room were not dark and the probe was for example a long green rectangle flashed (8 ms) on a red background. (b) Peri-saccadic mislocalization results adapted from Honda (1991). Note that for all locations tested, the probe is seen shifted in the direction of saccade before its onset and in the opposite direction after the saccade. (c) Peri-saccadic compression results adapted from Ross et.al (1997, 2001). All probes appear shifted toward the location of the saccade target. In order to compare effects between peri-saccadic mislocalization and compression, we normalized the locations by saccade amplitude.

While some authors suggested that peri-saccadic mislocalization reflects the remapping observed in electrophysiology literature (Burr & Morrone, 2011; Ross et al., 2001), others have found that the same effects occurs with simulated saccade (Ostendorf, Fischer, Gaymard, & Ploner, 2006) suggesting then that these effects are not linked to remapping. Some suggest that peri-saccadic mislocalization and compression reflect the combination of extra-retinal signal with the retinal persistence of the flashed probe, a model that provides a reasonable explanation of peri-saccadic

mislocalization (Pola, 2007). A more speculative model is however required to explain compression (Pola, 2011). Others have speculated that the addition of a motor feedback signal at the time of the flash interacts with the visual response in the case of the compression effects (Hamker, Zirnsak, Calow, & Lappe, 2008). Finally, some believe that mislocalization effects have no link to space constancy but rather reflect temporal and spatial uncertainty integration processes (Maij, Brenner, & Smeets, 2009, 2011) or the cortical magnification factor in retinotopically organized visual areas (VanRullen, 2004).

Even if the link between space constancy and mislocalization effects is unclear or perhaps non-existent, we will present in this thesis two studies involving the localization of visual targets across saccades. To understand the difference between these mislocalization results and our own, we present here a more detailed description of these effects.

Peri-saccadic mislocalization was first reported by Matin and colleagues using a two-alternative, forced choice procedure (Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970; Matin & Pearce, 1965). Several subsequent studies replicated the finding using a variety of techniques: by adjusting a cursor to the perceived location (Honda, 1991), by pointing to the screen (Bockisch & Miller, 1999; Miller, 1996) or by executing a second saccade to the perceived location (Dassonville, Schlag, & Schlag-Rey, 1995; Honda, 1985; Schlag & Schlag-Rey, 1995).

Several limits to the mislocalization effect were also reported. First, it appears that adding a visual reference, such as a map of Japan behind the target affects the amplitude of the effect (Honda, 1993), with a mislocalization of as much as 70% of the saccade amplitude in darkness (Dassonville, Schlag, & Schlag-Rey, 1992), reduced to 50% with visual references present (Dassonville et al., 1995; Honda, 1993). Second, while the timing of the flash relative to the saccade is critical, the flash duration is also important. For sequences of flashes presented during the saccade, the flickering dot was seen as an array of points whose individual locations corresponded to the mislocalizations seen for single flashes (Hershberger, 1987). However, if the flickering probe started flickering before the saccade, little or no mislocalization was reported, as if well-established position information overrode or stabilized any shifts that might have been seen for a single flash (Sogo & Osaka, 2001; Watanabe, Noritake, Maeda, Tachi, & Nishida, 2005). The pre-existing position information appeared then to outweigh the effects of peri-saccadic mislocalization seen with single flashes (Honda, 2006). Finally, mislocalization seems uniform (identical for different test locations across a screen, see Figure 4b) when tested in darkness or with limited references (Awater & Lappe, 2006; Honda, 1993; Lappe, Awater, & Krekelberg, 2000). However, in a well-lit environment, peri-saccadic compression – displacement of probes presented beyond the saccade target toward the saccade target – was observed (Lappe et al., 2000; Ross, Morrone, & Burr, 1997, see Figure 4c). This effect has been replicated several times, manipulating different visual aspects such as the number of bars perceived (Morrone, Ross, & Burr, 1997), the effect of probe contrast, color and shape (Lappe, Kuhlmann, Oerke, & Kaiser, 2006; Michels & Lappe, 2004), mislocalization of an object relative to a stable colored background (Lappe et al., 2006; Maij, Brenner, et al., 2011) or the reported distortion of the whole image (Ross et al., 1997, 2001).

Although making a saccade across a very brief flashed object seems like it might be limited to laboratory situations (but see Maij, de Grave, Brenner, & Smeets, 2011), mislocalization effects may inform us about the dynamic recalibration of location occurring around the time of a saccade. Some authors suggest that peri-saccadic mislocalization reflects a damped extra-retinal signal that is stretched in time (Dassonville et al., 1992; Schlag & Schlag-Rey, 2002) before being subtracted from retinal location to produce the predicted spatial location. However, that proposal only holds for the mislocalization of targets flashed in the dark but not for compression effects since the damped signal should give spatially uniform mislocalization effects. Finally this explanation has been recently challenged even for mislocalization in the dark, which was found to reverse in direction for longer duration probes (Jeffries, Kusunoki, Bisley, Cohen, & Goldberg, 2007). Also, recent work in electrophysiology suggests that the gaze-modulation of some retinotopicaly organized visual cells might explain peri-saccadic mislocalization (Morris, Kubischik, Hoffmann, Krekelberg, & Bremmer, 2012). For these authors, gaze-modulation could be reflecting the damped signal described by Dassonville et al. (1992). These results suggest that mislocalization effects reveal a brief moment of extreme spatial uncertainty around the time of a saccade, when other signals (such as eye in head signal) might play a bigger role than they do in a more stable environment.

Finally in the first and second study of this thesis (Szinte & Cavanagh, 2011; Szinte et al., 2012) we will show that mislocalizations are not found for long duration stimuli and that the effect also disappears if the stimulus exists before the saccade starts (as reported earlier by Honda, 2006). These results, together with the alternative explanations reported earlier, suggest that the link between mislocalization and space constancy remains unclear. Nevertheless, these mislocalization effects may yet reveal intermediate states of peri-saccadic processing.

3.3.2.3 Studies of trans-saccadic memory, integration and adaptation of visual features, locations and attention

In this section we ask what visual characteristics are maintained, stored and used across saccades and whether these characteristics might contribute to space constancy. We present here selected studies organized according to the type of information that is re-localized after the saccade. We start with trans-saccadic memory for visual content (object concepts, object shape, object size, number of elements); we then consider the trans-saccadic transfer of location, followed by studies reporting a potential transfer of sensitivity changes to particular features across saccades. We then end this section by describing more recent reports of the trans-saccadic transfer of attention.

Trans-saccadic memory and trans-saccadic integration of visual content were first addressed by McConkie and Zola (1979). These authors developed a model of an integrative buffer of visual processing during reading and discovered that altering the case of a block of text at the time of the saccade failed to produce any awareness that something was changed (see Grimes, 1996, for a review). Since then several other studies have examined the interactions between pre- and post-saccadic stimuli. Pollatsek, Rayner and Collins (1984) presented one drawing in the periphery which

was replaced by a second drawing at the fovea as soon as the observers saccaded to it. They found that information from the first picture facilitated the naming of the second picture, even if the second image differed in size or if it represented the same concept but was visually different (e.g. different pictures of a dog). Moreover, this facilitation effect was not altered when the a pre-saccadic object seen in the periphery was displaced to a different spatial location during the saccade (Pollatsek, Rayner, & Henderson, 1990), suggesting that the integration of content across a saccade was rather insensitive to position.

Trans-saccadic memory was also tested by the detection of image changes made at the time of a saccade. A high tolerance was found for object expansion and contraction (McConkie & Currie, 1996), for object rotation (Henderson & Hollingworth, 1999), and for changes in object sizes and colors in real-scene images (Grimes, 1996).

Finally, others tested the integration between pre- and post-saccadic images, examining whether two parts of a pattern could be fused despite the fact that they fell on very different locations on the retina before and after the saccade (Jonides, Irwin, & Yantis, 1982, 1983; O'Regan, 1992; O'Regan & Levy-Schoen, 1983). The results suggested that pixel-to-pixel integration does not occur. Nevertheless, some more global properties did show integration: the structural relations of object parts (Carlson-Radvansky, 1999; Carlson-Radvansky & Irwin, 1995); global object shape (Pollatsek et al., 1984), the relation between objects creating the orientation of a biological motion stimulus (Verfaillie, De Troy, & Van Rensbergen, 1994), and the integration of the global motion of random dot signals (Melcher & Morrone, 2003; but see Morris et al., 2010).

All of these results suggest that instead of a spatiotopic integration that is able to properly align and superimpose the contents of successive eye fixations (Breitmeyer et al., 1982; Jonides et al., 1982), trans-saccadic memory for visual content is more abstract and limited. This memory allows us to register visual object content under severe limitations, together with a coarse coding of object location (Irwin, 1992).

Trans-saccadic processing of location was tested by itself in a study by Bridgeman, Hendry and Stark (1975). In an experiment where observers reported the change in the location of a column of dots displaced very rapidly during the saccade, they found a very low probability of detection, especially when the shift occurred at the saccade onset.

This coarse coding of location was challenged in a study of Deubel, Schneider and Bridgeman (1996) who asked their participants to report the displacements of the saccade target that occurred during the saccade. They showed that contrary to the low accuracy of detecting a displacement of a target that was present when the saccade landed, adding a short blank of 50 milliseconds or more after the saccade, but before presenting the displaced target, dramatically improved displacement discrimination. This "blanking effect" might suggest that the pre-saccadic position was accurately coded and maintained across saccade but that some other process may have suppressed it when the target was present when the saccade landed.

That process has been called the saccade landscape theory (Deubel et al., 2002) and it is seen as a solution to space constancy without any use of efference copy. As previously described, a representation of the saccade target (and its surroundings) is acquired before the saccade and

when the saccade lands, the saccade landing area is searched for a match to the saccade target. If a match is found, that post-saccadic target location is taken to have the same spatial location as the pre-saccadic target. This explains why displacements during the saccade are not noticed – this process finds the target at its new location but assumes that it has not moved. Spatial coordinates are then recalibrated to that post-saccadic target location. However, if the target is not present when the saccade lands, then these authors propose that the visual system by default uses extra-retinal signals (Deubel et al., 1996) allowing accurate discrimination of any displacement.

In support of this proposal, the same authors examined what happened when (Deubel et al., 1998) a post-saccadically blanked target was presented without displacement together with a second target that was present when the saccade landed and which was displaced during the saccade. As predicted, the blanked target that had not moved was incorrectly seen as moving. The reason was that the target that was present as soon as the saccade landed was used as a landmark to reposition the post-saccadic spatial coordinates, ignoring the displacement. The “blanked” target was then necessarily seen as having moved in this new coordinate frame. This “landmark effect” was shown to be particularly effective for an object in the vicinity of the saccade target or vertically aligned with it (Deubel, 2004). The landmark effect, together with the blanking effect, suggests that post-saccadic target locations can be accurately predicted, but this information is only used if a match to the expected target cannot be made. When the target is present, it takes precedence in recalibrating post-saccadic spatial coordinates, ignoring the rare occasions where displacements may have occurred during the saccade (Deubel, Koch, & Bridgeman, 2010).

Next, we consider more recent experiments that have investigated the content of trans-saccadic memory by testing whether localized sensitivity to features might transfer across saccades. In these studies, after adapting to a particular feature at one location, a saccade was made and then a test stimulus was presented at the same position in space but at a different position on the retina. This procedure would test whether any neurons might respond to fixed locations in space either because they were part of a spatiotopic representation or because of the brief shifting of their receptive fields from the current to the expected location of the target (remapping). Spatiotopic aftereffects (the perception of the feature opposite to the one adapted) were initially found for example for motion (Ezzati, Golzar, & Afraz, 2008), faces (Melcher, 2005) and object tilt (Melcher, 2005, 2007). Contrary to the coarse models of trans-saccadic integration (Irwin, 1992), these results suggested that sensitivity to visual features might be transferred across saccades, or that a single cell (that shifted receptive field location across a saccade) was adapted. However, subsequent studies partly failed to replicate these studies, casting doubt on the transfer of sensitivity to visual features across saccades (Afraz & Cavanagh, 2008; Knapen et al., 2009, 2010; Wenderoth & Wiese, 2008).

Finally, we consider here a recent suggestion that spatial attention is correctly re-allocated to an attended target’s post-saccadic location (Cavanagh et al., 2010; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). The target-related activity peaks on retinotopic visuo-motor maps have been shown to convey attentional benefits to the target locations (Awh et al., 2006; Moore & Armstrong, 2003).

However, since these are retinotopic representations, each eye movement will shift the attention benefits away from the target's spatial location. The remapping process then shifts the activity peak to the retinal location that corresponds to the location where the target is expected after the saccade. The attentional benefits follow. This remapping of attention pointers then puts the peaks of activity into alignment with the target's spatial position.

This repositioning of attention peaks was indeed tested directly in several studies using visual cues presented before saccades to test post-saccadic attentional benefits at the spatial and retinal locations of the cue (Golomb, Chun, & Mazer, 2008; Golomb et al., 2008; Mathôt & Theeuwes, 2010). These authors showed that attention is reallocated to the spatial position of the cue with however a residual shift at the retinal location for the first 100 ms following the saccade. Finally, Rolfs et.al (Rolfs et al., 2011) in a study using attention peaks for subsequent saccade targets showed that before the eyes start to move, attention is remapped to the position it will have after the saccade. This suggests that the remapping of peak activity allows the correct reallocation of attention at the spatial position of the target.

A further suggestion is that these target-related peaks in visuo-motor maps not only specify the location to which a saccade will be directed (overt attention), and the location to which attentional benefits will be directed if no saccade is executed (covert attention), they also specify the location at which the attended target will be perceived. This proposal underlies our use of location measures to examine the remapping processes that correct for eye and head movements. To access these visuo-motor locations (attention pointers) around the time of a saccade or head movement, we present a probe before the movement and one after and we ask subjects to report the direction of motion or displacement that they see. If remapping processes update the position of the first probe to predict where it should be seen after the eye movement, then when it is not there but is presented at a second location, the subjects should see this offset as apparent motion and that motion should be seen in spatial not retinal coordinates. Any inaccuracies in remapping will then be seen as deviations from the veridical motion direction.

This suggestion is supported by the results of a clever set of experiments by Rock and Ebenholtz (1962) that evaluated whether apparent motion could be experienced even in the absence of retinal motion. They demonstrated that visual probes presented in the periphery at the same position on the retina but different positions in space (because of an intervening saccade), can be experienced as motion in spatiotopic coordinates, indicating a correction of the location of the pre-saccadic probe. This result, replicated more recently (Szinte & Cavanagh, 2011) for two dot probes as well as for more complex shapes (Fracasso, Caramazza, & Melcher, 2010; Melcher & Fracasso, 2012) clearly shows that the effect of saccades on perceived locations are corrected. This proposal that remapping updates location for perception, as well as for saccades and attention, implies that apparent motion, the perception of motion between two stimuli offset in time and space, depends on attention. This is actually quite an old proposal originally made by Wertheimer (1912) and supported by a variety of more recent articles (e.g. Dick, Ullman, & Sagi, 1991; Verstraten, Cavanagh, & Labianca, 2000). In this proposal, the shift of attention generates the impression of motion. These results support the idea that apparent motion is a valid measure to use to examine the remapping of attention and perceived location across eye and head movements.

These suggestions will be addressed in different studies reported in this thesis and also in the last paragraph of the introduction in which we will present our model of space constancy driven by shifts of spatial attention at the time of a saccade.

Of these different trans-saccadic studies from psychophysics we find a number of characteristics of what is retained across a saccade. Although a spatiotopic buffer does not seem to exist, some abstract information may be retained across saccades as illustrated by the idea of an object file (Kahneman, Treisman, & Gibbs, 1992). Trans-saccadic integration could then reflect a higher level of processing (e.g. probability summation) as a recently suggested by Morris et al (2010). In contrast, studies of location and spatial attention show an accurate repositioning of this information across saccades.

3.3.3. Evidence from electrophysiology

3.3.3.1 Saccadic suppression

Here we briefly summarize selected studies that allow us to distinguish between the two proposals for the origin of saccadic suppression (i.e. visual masking and perturbation from the efference copy). Saccadic suppression has an impact on the problem of space constancy as it suppresses information during the saccade that might be useful for solving the correspondence between pre- and post-saccadic images. Although the studies presented in this thesis do not directly address the effects of saccadic suppression, it of course occurs in all our conditions with saccades. For that reason, we think it is helpful to review its definition, limits and physiological origins.

Psychophysical studies have given evidence for the extra-retinal origin of the effect as well as demonstrating a difference in the strength of suppression between stimuli carried by the magnocellular and parvocellular pathways. These effects were tested in monkeys by studying the modulation of cell activity at the time of the saccade. Clear modulation of cell firing rates in the lateral geniculate nucleus (LGN) was found well before and continued up to 50 ms after the saccade (Reppas, Usrey, & Reid, 2002; Royal, Sáry, Schall, & Casagrande, 2006). The initial effect was a weak suppression followed by a large enhancement just after the saccade (when visual activity arrived in cortical areas of the brain). Contrary to the idea that saccadic suppression is due to a reduction of magnocellular but not of parvocellular cell responses, magnocellular cells showed an enhancement during the saccade, while parvocellular cells showed no modulation in firing rates between saccade and fixation conditions (Ramcharan, Gnadt, & Sherman, 2001). These results suggest that the LGN was only partly involved in saccadic suppression. However, one study recently challenged these findings, showing reduced activity around the time of a microsaccade, both for parvo and magnocellular neurons of the LGN (Saul, 2010).

The same pattern of results was also found when testing for neural correlates of saccadic suppression in V1. A clear absence of modulation or only moderate suppression was found initially (Fischer, Boch, & Bach, 1981; Wurtz, 1968) but more recent saccade and microsaccade studies show both behavioral suppression of detection and neuronal suppression of V1 cells (Hass & Horwitz, 2011; Kagan, Gur, & Snodderly, 2008).

Strong suppressive modulation was found in cortical motion-coding areas such as the middle temporal –MT– and medial superior temporal –MST– areas (Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Thiele, Henning, Kubischik, & Hoffmann, 2002), in the inferior division of the pulvinar –PI–, (Berman & Wurtz, 2010) as well as in the superior colliculus –SC– (Richmond & Wurtz, 1980; Robinson & Wurtz, 1976). These results suggest a potential set of structures and pathways for saccadic suppression (LGN-V1-MT-MST, see Wurtz, 2008; SC-PI-MT-MST, see Wurtz, McAlonan, et al., 2011). However, no results from these articles have identified the retinal or extra-retinal signals that trigger the saccadic suppression.

Some progress in this direction was made in two studies by Wurtz and colleagues. First, they compared the effects of visual masking with and without saccades and showed that the masking alone, in the absence of a saccade (without extra-retinal signals), partly explained the suppressive activity in V1 seen with a saccade (Judge, Wurtz, & Richmond, 1980). On the other hand, a second study showed that the suppression of background activity persisted when monkeys attempted to make a saccade but could not because their eye muscles were paralyzed (Richmond & Wurtz, 1980). This result suggested that a copy of the motor command (efference copy or corollary discharge) was triggering suppression even when the saccade could not be executed.

Overall, these results suggest that both masking and extra-retinal signals contribute to saccadic suppression. Additional studies are need to link the suppressive modulation of visual cells with the perceptual effects of saccadic suppression (Wurtz, McAlonan, et al., 2011).

3.3.3.2 Remapping and corollary discharge

As described previously, a series of fundamental physiological discoveries has brought new interest and ideas to the topic of space constancy. The studies described in this section show that visual targets can be represented in visual areas that are retinotopic because their locations are updated to track the target's spatial locations across eye movements. The studies support the proposal that the updating process is a remapping mechanism that uses the efference copy of the motor signal. This mechanism, that operates only on a few attended targets, is today thought to contribute to space constancy (Wurtz, 2008) even though this link is not yet well established.

The central purpose of this thesis is to link physiological and psychophysical evidence concerning the mechanisms that contribute to space constancy. The purpose of this section is to clarify the discoveries made in single cell recordings, discoveries that we will later use to describe our model of space constancy based on the remapping of attention pointers.

These discoveries summarized in this section were mostly inspired by and follow from the key study of Duhamel, Colby and Goldberg (1992) who first linked the previously reported trans-saccadic memory effect (Gnadt & Andersen, 1988; Goldberg & Bruce, 1990) of neurons of the lateral intraparietal area (LIP) to the updating of target locations across saccades.

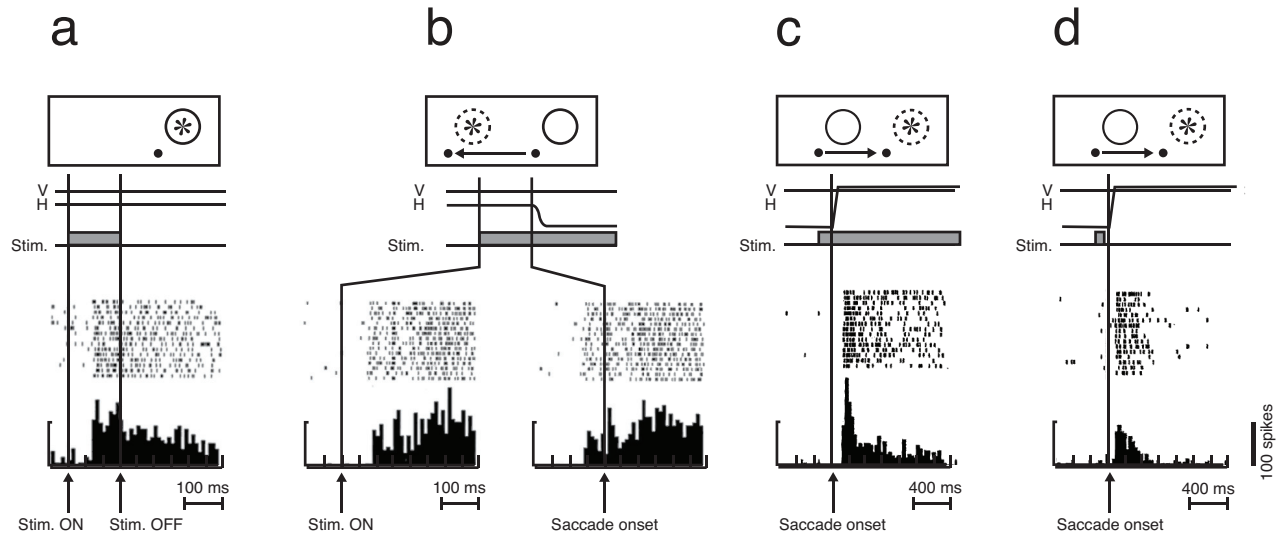


Figure 5. Physiological remapping in LIP. Diagram in each panel shows the fixation and saccade target (black dots), the visual stimulus (star), saccade (arrow), and the receptive field location before (circle) and after the saccade (dashed circle). The time line below the stimulus configuration shows the vertical (V) and horizontal (H) eye position, the beginning and end of the stimulus (stim.). Below the time lines are raster plot diagrams with each dot being a cell discharge and each line being a trial. Spike density histograms are shown beneath each raster plot. Raster plots and histograms are aligned on the event indicated by the long vertical line. The bold line to the right indicates 100 spikes. (a) In a simple fixation task a neuron responds to a stimulus presented in its receptive field with a visual latency of 70 ms. (b) In a saccade task, a stimulus is presented at the position where the neuron's receptive field will be after the saccade. Data are aligned in the left panel on stimulus onset and in the right panel to saccade onset. The neuron responds predictively and fires 80 ms before the eye movement, thus 150 ms (80 ms + 70 ms) before its normal reaference response. (c) Only a subset of LIP cells show predictive activity. As shown in this panel for another neuron, responses begin when the stimulus enters the receptive field. (d) The same cell discharges when the saccade displaces the receptive field to where the stimulus was previously flashed, even thought the stimulus is no longer present. This result reflects a remapping of remembered stimuli, a result found in the majority of LIP cells. Adapted from Duhamel et.al (1992).

In this 1992 article, the authors recorded the latency and magnitude of response to a visual stimulus presented inside neural receptive fields while the animal fixated (Figure 5a). On saccade trials, animals made an eye movement and a second stimulus was presented at the "future field" location, the position in space where the receptive field would be after the saccade (Figure 5b). This location typically fell far outside the neuron's receptive field. Nevertheless, the neuron responded and its response started even before the eye brought the stimulus inside its receptive field. This predictive activation could not be attributed to the saccade or to the stimulus itself and was obtained for many neurons tested, though not all (see Figure 5c). However, a memory response (not predictive) to a stimulus that was briefly flashed at the position the receptive field would have arrived following the saccade (see Figure 5d) was observed in almost all the cell tested in LIP by these authors.

Duhamel and colleagues concluded that their results reflected the updating of the location of the stimulus at the time of a saccade, a brief "remapping" of neuron's receptive field to the location that it would have had after the next eye movement. Remapping was proposed to maintain the spatial alignment between the external world and its internal representation. Remapping was initially studied in the lateral intraparietal area (Colby, Duhamel, & Goldberg, 1996; Duhamel et al., 1992; Gnadt & Andersen, 1988; Goldberg & Bruce, 1990; Heiser & Colby, 2006; Kusunoki & Goldberg, 2003). It was then observed in subsequent saccade related areas such as the frontal eye fields (Sommer & Wurtz,

2006; Umeno & Goldberg, 1997, 2001) and the superior colliculus (Walker, Fitzgibbon, & Goldberg, 1995), as well as in extra-striate visual areas such as V4, V3A, V3 and V2 (Nakamura & Colby, 2002; Tolias et al., 2001).

As described in a previous section, remapping reflects a transfer of activity from a population of neurons representing the stimulated attended location to another population of neurons representing the location the stimulus will have after the saccade (Berman & Colby, 2009). Remapping was found to be effective in a few milliseconds for some neurons (Berman & Colby, 2009; Duhamel et al., 1992). However other studies showed that some cells had a dual responsiveness to the both the actual and the next position of the receptive field (Kusunoki & Goldberg, 2003; Nakamura & Colby, 2002; Sommer & Wurtz, 2006). These results suggest that the transfer takes time but is generally completed at the time that the saccade has landed (Kusunoki & Goldberg, 2003).

One of the most interesting aspects of remapping outlined in the key paper of Duhamel et al (1992) was that updating could be *predictive*, that is, the cell would respond to the stimulus before it arrived in its receptive field. This anticipatory response suggests that cells showing updating activity do not wait for the retinal or proprioceptive signals which would be available only during or after the saccade, but instead rely on the efference copy of the motor command (Sperry, 1950; von Holst & Mittelstaedt, 1950). This would be the only signal available before the saccade to trigger the remapping. Sommer and Wurtz demonstrated a pathway for the efference copy (Sommer & Wurtz, 2000, 2002) from the superior colliculus to the frontal eye fields via an intermediate step in the thalamus, the medial dorsal thalamic nucleus (MD). They showed that the efference copy arriving through this pathway was linked to the guidance of the saccade in a double-step saccade task, such that an inactivation of MD reduced the accuracy of the second saccade (Sommer & Wurtz, 2002). They suggested that the pathway therefore conveys crucial information for the remapping of cell activity in the frontal eye fields (Sommer & Wurtz, 2006).

As described by Wurtz in several reviews (Wurtz, 2008; Wurtz, Joiner, & Berman, 2011; Wurtz, McAlonan, et al., 2011), a key finding missing from the electrophysiology of remapping is the link between this predictive transfer and space constancy. Nevertheless, different reviews linked remapping to several different effects reported in psychophysical studies. For example, it was speculated that the shift of receptive field sensitivity explained the mislocalization effect observed for targets flashed at the time of the saccade (Burr & Morrone, 2011; Ross et al., 2001) as well as spatiotopic adaptation and integration effects (Melcher & Colby, 2008).

Wurtz and colleagues (Wurtz, 2008; Wurtz, Joiner, et al., 2011) also suggested that the remapping process mediates the comparison between the pre and post-saccadic information that is required in the trans-saccadic memory hypothesis of spatial constancy (e.g. Deubel, et.al, 2002). Specifically, Wurtz and colleagues proposed that saccade landscape theory (and also the related saccade target and calibration theories) were driven by the efference copy because both blanking and landmark effects (Deubel, 2004; Deubel et al., 1998) suppose a comparison between the pre- and

post-saccadic targets. This comparison would correspond at the physiological level to the remapping of activity between the pre- and post-saccadic target retinal locations. One problem with this proposal is that saccade-target theory requires a mechanism to match pre- and post-saccadic target images (Deubel et al., 2002) and this is unlikely to exist in the visuo-motor related areas (Wurtz, Joiner, et al., 2011). In contrast, Cavanagh and colleagues (2010) suggested that remapping centers maintain, across a saccade, a set of potential locations as peaks of activity, conferring attentional benefits at the corresponding retinotopic location in early visual cortices (Awh et al., 2006). In this proposal, remapping served to update target locations in saccade areas, the target location then allowed a rapid post-saccadic access to the attended object features.

3.3.4. Evidence from human brain imagery and EEG-MEG

3.3.4.1 Functional MRI studies

Remapping is established as a clear phenomenon observable in animals with the high temporal and spatial resolution of electrophysiology. In this section we will consider how we could test whether target-related activity is transferred to the expected post-saccadic location around the time of a saccade using fMRI. We will consider whether a technique with a very low temporal resolution can really pick up such a brief transfer of activity that in macaques would last perhaps less than a few hundred of milliseconds. We will then consider what fMRI data can add to the animal studies if this were possible.

Several authors have challenged the issue of temporal resolution and designed experiments where, instead of looking for a transfer of activity surrounding the saccade onset as electrophysiology found, they used inter-hemispheric transfer of stimuli that disappear before saccades (a result also found in electrophysiology). They then looked for either remembered movements (Medendorp, Goltz, & Vilis, 2006; Medendorp, Goltz, Vilis, & Crawford, 2003) or remembered attended stimuli (Merriam, Genovese, & Colby, 2003, 2007), which across saccades could possibly evoke a change in blood-oxygenation level dependent (BOLD) activity in the ipsilateral brain hemifield.

For example, Merriam et al (2003) exploited the laterality of different human visual areas by presenting, in the left visual hemifield, a large attended target that disappeared before the execution of a saccade. The observers made, for example, a saccade across the target to a position further to the left. This was chosen because it would bring the location of the target into the right visual hemifield if the target had still been present when the saccade landed. At fixation, prior to the saccade, the target would evoke a change in BOLD signal in the contralateral hemisphere (right hemisphere), whereas its remapped activity should be in the ipsilateral hemisphere (left hemisphere). The authors found this expected activity in the ipsilateral hemisphere, a signal that could have no other source than the remapped representation because there were no stimuli presented at any time in the corresponding visual field. The same rationale was followed for a double saccade task with a second saccade target that could be remapped either while remaining in the same or in a different hemisphere (Medendorp, Goltz, et al., 2003).

These results indicate that the activity of remembered target sweeps were transferred from one hemisphere to the other. These findings are impressive given the low temporal resolution of functional imaging and the brief time course of the remapped activation. The increase of BOLD response related to the remapped activity was seen in the posterior parietal cortex (Medendorp, Goltz, et al., 2003; Merriam et al., 2003) as well as in earlier visual areas with more robust signal in the extrastriate visual areas (Merriam et al., 2007). These results extend the single-cell findings of remapping in monkey to the human brain. However, because of the very long time constants of fMRI, there is no way to test if predictive remapping is seen prior to the eye movement.

3.3.4.2 MEG-EEG studies

Contrary to functional MRI, electroencephalography (EEG) and magnetoencephalography (MEG) have good temporal resolution and should therefore be appropriate techniques to record the pre-saccadic transfer of activity in humans, as has been observed with remapping in monkey physiology.

To our knowledge, only one study has investigated saccadic updating with MEG (Van Der Werf, Jensen, Fries, & Medendorp, 2008). This study examined the oscillatory activity in the parietal cortex in a delayed anti-saccade task designed to disambiguate the saccade goal from the presented visual target. The study reported both a contralateral activity related to the memory of the target and sustained ipsilateral activities reflecting a remapping of a motor goal representation. However as with the fMRI studies, these activities reflected post-saccadic memory of a stimulus that had been removed before the saccade rather than the predictive transfer of activity reported in electrophysiology even prior to the eye movement.

EEG has been used to identify this predictive signature of remapping in humans. Several studies based on experimental procedures similar to those used in fMRI studies initially failed to find any pre-saccadic activity (Bellebaum & Daum, 2006; Bellebaum, Hoffmann, & Daum, 2005; Parks & Corballis, 2008). Indeed, these studies reported several electrical signatures of trans-saccadic activity, but these signatures were in the wrong hemisphere (contralateral), or arrived too late to reflect predictive remapping (Bellebaum & Daum, 2006) or rather reflected motor preparation rather than updated remapping (Parks & Corballis, 2008; Peterburs, Gajda, Hoffmann, Daum, & Bellebaum, 2011).

Nonetheless, in a more recent study Park & Corballis (2010) did find a correlate of predictive remapping. They used a subtraction method of the saccade related activity and found, for a selected portion of electrodes over the parietal cortex, the expected pre-saccadic ipsilateral enhancement preceding the execution of a saccade.

EEG-MEG and fMRI studies have reported evidence of memory based and predictive remapping in human cortical areas analogous to those reported in monkeys. These studies therefore support the theory that remapping may serve to space constancy.

3.4 Updating target locations across head movements

It is not only our eye movements that change the image on the retinas, head and body movements do so as well, and quite often, the head and eyes move together to orient to a new target. How does our visual system deal with the consequences of a head movement? Typically, we do not experience an unstable world when our head moves, any more than we do when our eyes move.

Nevertheless, it is interesting to note that there is no process like saccadic suppression that occurs during head movement so that optic flow seen during the head movement may contribute to any corrective processes. However, the eyes seldom sweep over the scene in tandem with the head. Typically, reflexive eye movements (e.g., the vestibulo-ocular reflexes) maintain fixation on a given point, keeping the retinal image relatively stable, until a saccade is made to a new fixed point. To the extent that these reflexive eye movements maintain a steady retinal image as the head moves, there is little additional change to correct for beyond the changes created by the saccades. In this case, the magnitude of the head movement is the same as the sum of the sequential eye movements. Corrections for each of the sequential eye movements through the remapping processes that we have already discussed would then maintain accurate representations of target locations without any residual head movement to correct.

However, there are head movements that change the retinal image that do not allow reflexive eye movements to maintain a steady image as the head moves. Specifically, a roll movement where the head rotates around the visual axis happens whenever we tilt our head while maintaining fixation on a target. A forward or backward motion of the head, again along the visual axis, occurs whenever we approach a target or step away from one. In both these cases, fixation is maintained on a target but the retinal image is not stabilized during the head movement. It rotates (for head roll), or expands or contracts (for fore-aft motions). In these cases, optic flow from retinal information may contribute to estimating and correcting for the head movement. However, there are several other signals available such as efference copy from the motor commands that move the head, proprioception from the neck muscles and articulations and from the vestibular organs. We summarize here the research on corrections of location perception for head movements, research that shows evidence of the contributions from efference copy signals as was seen for eye movements (but now for head movements) but also some additional ones.

3.4.1. Signals for ”remapping” across head movements

The head can move in many ways and these movements are accompanied by an array of signals. Some of these signals are like those available for eye movements; others are not. The motor commands to the neck and body muscles can trigger efference copy signals, as do the commands to the eye muscles. Certainly the consequences of a head movement on the retinal image will generate retinal cues of optic flow just as eye movements do, although now not subject to suppression during the movement. However, in addition to these, there are proprioceptive signals from the stretch receptors in the neck, torso muscles and joint articulation signals. Moreover, a specific sub-cortical structure in

the inner ear generates characteristic signals for head and body movements: the vestibular system (see Cullen, 2012 for a recent review on that structure).

The vestibular system is composed of three roughly orthogonal semicircular canals and two otolith organs (the utricle and the saccule). These substructures sense, respectively, rotational movements (or angular velocity) and linear acceleration (including the gravitational force). The vestibular system can then relay information about rotation (via the semi-circular canals) and translation (via the otoliths) of the head.

Among these signals we can make a first distinction between those available before the head movement and signals that are available at the time of the head movement. Only efference copy can convey information about head movements to the visual system before the head movement starts. Proprioceptive, retinal and vestibular signals are all generated as the head moves, and thus involve a certain delay before they convey accurate information of the movement in progress.

3.4.2. Empirical evidence of the compensation for head movement

The following studies have evaluated the extent to which the remembered location of a target was corrected for a subsequent head movement. These head movements were either performed voluntarily (active movements) or effected with the use of specialized motion platforms that passively rotate or translate the subject in space (passive movements). In order to determine the contribution of different signals to accurate location judgments we will compare the findings concerning head movement compensations for active versus passive head movements. This comparison is particularly useful because efference copy is only available for active movements of the head, not passive movements. The principal outcome is that location judgments are accurately corrected for almost all rotational and translational head movements. However, this is true for both active and passive head movements indicating that efference copy appears to play only minor role in achieving this accuracy. Finally, the studies show that the vestibular system is essential at least in correcting for head roll and head fore-aft translations.

Almost all the experiments described in this section evaluated the accuracy of a delayed action (saccade or pointing) made in the spatial direction of a probe briefly presented before the occurrence of a head movement. In order to eliminate undesired vestibulo-ocular reflexes, head movements were always executed or sustained while the subject fixated a central target (however, recall that this sustained fixation does not stabilize the location of the briefly presented target for head roll or head fore-aft translation). All evaluations of the updating of target location across head movement were based on the accuracy of pointing to or saccading to this memorized location in space once the head movement was completed. These findings may then not be a general property of everyday correction for head movement where the important point is our perception of where things are as the head movements are made.

3.4.2.1 Active head movements

For active head movement, the judgments of remembered test probe locations were generally accurate across both rotational and translational head movement. For example while observers held their heads tilted to the right, a target was flashed and they were instructed to saccade to it after moving back their heads to the initial location. Under such conditions, observers made accurate saccades to the remembered location, revealing a nearly perfect compensation for head roll (Medendorp, Smith, Tweed, & Crawford, 2002). Similar conclusions were made for active head yaw following a slightly different method (Blouin, Gauthier, van Donkelaar, & Vercher, 1995; Blouin, Labrousse, Simoneau, Vercher, & Gauthier, 1998). Finally, Medendorp, Tweed, and Crawford (2003) tested active lateral translation with targets and fixation on different depth planes, which involves a more complex geometry for updating (motion parallax), and still found that the subsequent saccade fell mainly on the spatial location of the previously flashed target, suggesting an accurate compensation processing.

Based on these results, Medendorp and colleagues (2002; 2003) suggested that remapping might be a possible mechanism to explain the accuracy observed. They noted that updating for rotation and translation could not be explained by a simple linear subtraction mechanism. Instead, they propose a process involving the rotation or translation of the stored target through the inverse of the eye's movement in space (Medendorp et al., 2002; Smith & Crawford, 2001), a mechanism that would explain the accurate updating observed in the case of non-commutative movements (Glasauer & Brandt, 2007; Klier, Angelaki, & Hess, 2007).

3.4.2.2 Passive head movements

If the head is moved passively, efference copy signals will no longer be available. Recall that passive movement of the eye (by pushing it) makes the world unstable. What happens for passive movement of the head? To test this, a series of experiments in both human and monkeys tested the remembered location of a target that was presented briefly before passive head or whole body movements.

For a passive rotational movement, accurate, or fairly accurate, updating was found for single yaw rotation (Israël, Ventre-Dominey, & Denise, 1999; Klier, Hess, & Angelaki, 2006; Li, Wei, & Angelaki, 2005; Mergner et al., 2001), and yaw rotation following a pitch or a roll movement (Glasauer & Brandt, 2007; Klier et al., 2007). Less accurate, but still good, updating was found when incongruent active head and passive torso yaw rotation were applied (Blouin et al., 1998).

For head and body passive roll, several studies reported accurate or almost prefect updating of the remembered flash location (Bloomberg, Jones, & Segal, 1991; Klier, Angelaki, & Hess, 2005; Klier et al., 2006; Li et al., 2005).

For passive translation movement, again human observers and monkeys show accurate compensations for lateral translation (Klier, Hess, & Angelaki, 2008; Li et al., 2005) as well as for fore-aft translations (Berthoz, Israël, Georges-Francois, Grasso, & Tsuzuku, 1995; Israël & Berthoz, 1989; Klier et al., 2008; Li & Angelaki, 2005).

Thus, contrary to what would be expected if efference copy were the only source for updating locations, compensations of passive movements were found to be as accurate as compensations for active movements. With active movements, gain (the proportion of correction) across observers was 0.91 ± 0.2 (Medendorp, Tweed, et al., 2003) whereas for the same movement executed passively, it was 0.84 ± 0.28. Neither result differed significantly from perfect gain of 1.0. The same was also true for head or body roll with gains approaching 1 for active (Medendorp et al., 2002, gains were not reported but could be determined graphically) and passive (gain of 0.92 ± 0.37, Klier et al., 2006) movements. These results suggest that proprioceptive and vestibular signals are of major importance for memory updating across head and body movements, while efference copy makes little or no contribution.

Some authors have also examined the role of vestibular signals in correcting for head movements, either by surgically removing the vestibular system in monkeys or by finding labyrinthectomized human patients or by manipulating the gravitational cues to compare updating in upright and supine positions. The outcomes of these studies are that corrections for fore-aft translation are severely impaired in labyrinthectomized monkeys (Li & Angelaki, 2005; Wei, Li, Newlands, Dickman, & Angelaki, 2006) and humans (Israël & Berthoz, 1989) suggesting that accurate correction for linear translation of the head requires vestibular information of self-motion. On the other hand, while updating for yaw rotation and lateral translation were compromised following the surgery, the corrections for these head movements improved over time to return to a normal level within a few months (Wei et al., 2006). Moreover, gravitational cues from the otoliths seem to be important when correcting for head roll movement since accuracy was drastically reduced in a supine condition where rotation causes changes detected only by the semicircular canals. This influence of gravity did not generalize to yaw rotation, however, where equal performance was found in both upright and supine body positions (Klier et al., 2006).

To conclude, updating the remembered location of a target to correct for head movements relies on a multitude of signals. When efference copy is used in active head movement compensation, its effect seems limited and a combination of vestibular and proprioceptive signals seems to better explain the correction of remembered locations for head movements, as evaluated by a subsequent saccade or pointing movement. However as pointed out earlier, these studies all evaluate locations based on delayed actions. This delay might leave enough time for optic flow, reaference, proprioceptive, and vestibular signals to contribute. In contrast, in everyday situations, space constancy is needed and appears to be present in real time. The lack of contribution from efference copy might also be a consequence of the delayed report procedure. Nevertheless, Klier et al (Klier et al., 2008) suggest that an efference copy of the vestibulo-ocular reflexes that maintain the eye at fixation might provide another feedback signal. Such feedback could nevertheless not contribute to predictive corrections (Klier & Angelaki, 2008; Medendorp, 2011), as these signals are not available before the head movement.

3.5 Attention and saccade planning

Physiological and psychophysical studies generally define “spatial attention” through its effect on visual perception. It is seen as a re-locatable allocation of processing resources to a given location of our visual field, measured behaviorally as an improvement in discrimination or sensitivity at that location, together with a decrease of performance at unattended locations. Physiologically, it is measured by a modulation of cell activity at the attended (task relevant) location (Carrasco, 2011; Treue, 2003). Although it is not our purpose to review the history of spatial attention research, it is important to specify the well-known distinction between overt and covert attention. These describe perceptual and neuronal enhancements seen for a target object that is either brought to the fovea by an eye and/or head movement (overt attention), or attended to in the absence of orienting motor behavior (covert attention).

Although the basis of spatial attention is not clearly understood, several similarities between overt and covert attention at both the psychophysical and electrophysiological level suggest that attention in its broader sense might help keep track of target locations across movements of the head and eyes. The following paragraphs summarize evidence for the link between eye movement planning and attention.

3.5.1. Psychophysical evidence of a link between attention and saccades

Certainly the most direct proposal of a connection between covert attention and eye movement is the pre-motor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994). In a series of experiments Rizzolati and colleagues first showed a bigger cost for the allocation of attention on an uncued location in the opposite hemifield rather than in the same hemifield as the cue (Rizzolatti, Riggio, Dascola, & Umilta, 1987), as well as an influence of attention on saccade trajectories (Rizzolatti et al., 1994). Based on these results Rizzolati et al proposed that the system controlling motor action is the same as the one controlling spatial attention.

Different authors demonstrated later an obligatory and selective coupling of visual attention and saccade target selection. First in a dual task paradigm where observers saccade to one location and detect a target letter at another, Hoffman & Subramaniam (1995) observed that discrimination performance was best when the saccade target and the detection target shared the same location and that subjects were unable to completely dissociate the attended and the saccade location. In a related experiment, Kowler et al (Kowler et al., 1995) found that letter identification was better at the saccade goal than at any other position. They also found that observers could not saccade accurately to one location while at the same time making accurate letter identifications elsewhere.

These results provided the first evidence of a coupling between visual attention and the selection of a movement goal, followed a year later by the study of Deubel & Schneider (1996). There, observers were asked to attend to a specific location presented in the periphery while they executed a saccade either to the same or to a nearby location. During saccade preparation, a target was briefly presented at the attended location. Even if the subject knew in advance where the target would appear, good performance was only found when the eyes were directed to the object to be identified. These results

suggested an obligatory coupling between spatial attention and saccade programming, leading the authors to conclude that a single mechanism drives both the selection made by visual attention and the position information for the motor response.

3.5.2. Neuronal evidence of a link between attention and saccades

At the neuronal level, the visual attention and oculomotor systems are known to be highly interconnected. Several structures involved in motor coordination (such as the superior colliculus and the frontal eye fields) are also some of the structures presenting the activity modulations that defines visual attention at the neuronal level (Wurtz, Sommer, Paré, & Ferraina, 2001).

Several laboratories have demonstrated this link explicitly by combining micro-stimulation with psychophysical and electrophysiological measures. In both the frontal eye fields and the superior colliculus, microstimulations that evoked eye movements to a specific retinal location also, when delivered at subthreshold levels, evoked the typical effects of visual attention, localized at the corresponding location. These effects were either an increase in luminance sensitivity (Moore & Fallah, 2001, 2004), in motion sensitivity (Müller, Philiastides, & Newsome, 2005) or in a monkey's ability to detect changes in a visual display (Cavanaugh & Wurtz, 2004). These attentional effects, very similar to those found in simple cueing experiments (Treue, 2003), suggest that motor planning areas have a causal role in directing the covert visual selection of targets. Finally in an elegant experiment, Moore & Armstrong (2003) demonstrated that the same subthreshold microstimulation at a particular location in FEF increases cell response at the corresponding location in early visual cortex (V4). These findings suggest that the gain of visual responses in extrastriate cortex might reflect a direct attentional modulation from saccade maps, corresponding to the effect observed when saccade are planned to a visual target (Deubel & Schneider, 1996).

3.6 Remapping of attention pointers

Here, we will first describe the link between attention and remapping. Then we will demonstrate that the behavioral measurement of attentional benefits is an appropriate method to evaluate remapping on retinotopic maps and its role in recovering target locations in the world despite eye and head movements. For that purpose we will describe a model of space constancy based on the displacement of attention pointers and finish with the different predictions and questions that this model generates.

3.6.1. The link between attention, remapping, and space constancy

Here we consider whether remapping, the correction of target locations for the effects of eye and head movements, is a potential contributor, and perhaps the most important or even sole contributor, to space constancy (Wurtz, 2008). We first note that visuo-motor maps, on which remapping operates, might more appropriately be considered attention maps, as described in the previous section (see also these reviews, Goldberg, Bisley, Powell, & Gottlieb, 2006; Gottlieb, 2007; Moore, Armstrong, &

Fallah, 2003). The saccade/attention maps not only encode the locations of potential saccade targets, they direct attentional benefits to those locations (Moore & Fallah, 2004). So, as shown in the studies of Rolfs et al (2011), remapping operates on and can be seen in the allocation of attention. So in linking remapping and space constancy, we are also linking attention and space constancy.

But here we must deal with an enormous mismatch in scale. Specifically, when our eyes move, the whole world appears stable. Not just little portions of it. In contrast, a primary characteristic of attention is its limited capacity. Only a few targets can be attended at the same time (see Carrasco, 2011 for a recent review). How can a mechanism such as attention, which operates on a small number of items, be considered to be part of a solution to a process, visual constancy, which appears to apply to all items in the visual field? There are two lines of evidence that support this unlikely link.

First, despite subjective experience to the contrary, visual constancy does not involve the entire visual scene but only a few attended portions of it. Specifically, any number of items in a scene can be changed at the time of the saccade (Grimes, 1996; Henderson & Hollingworth, 1999) without observers noticing unless bottom-up or top-down attentional mechanisms are directed to those items (Cavanaugh & Wurtz, 2004). We are unaware of changes to unattended items that occur across saccades (O'Regan, 1992; Rensink et al., 1997) so models of space constancy do not have to deal with the entire visual scene, but only with the attended items in that scene (Berman & Colby, 2009; Wurtz, 2008).

A second line of evidence shows as well that remapping is not found for all elements in the visual scene either. A stable and irrelevant target that falls post-saccadically in a receptive field does not trigger any remapping in LIP cells (Colby et al., 1996; Duhamel et al., 1992). However, if the same target draws attention by a transient entering the same receptive field, it evokes strong and predictive remapping activity (Gottlieb et al., 1998).

So potentially, space constancy might be mediated by remapping the locations of only attended items. Even though this may be sufficient, there may be many other critical contributors to space constancy. We will however not address these in this thesis, we examine only remapping.

3.6.2. Remapping of attention pointers

A model described and tested earlier (Cavanagh et al., 2010; Rolfs et al., 2011), proposed that remapping shifts the locations of attentional pointers that index a few attended objects, updating their positions to correct for eye movements. This model initially involved only eye movements, however since it calls on remapping in visuo-motor areas, it could also take into account the effects of head movement (Medendorp et al., 2002).

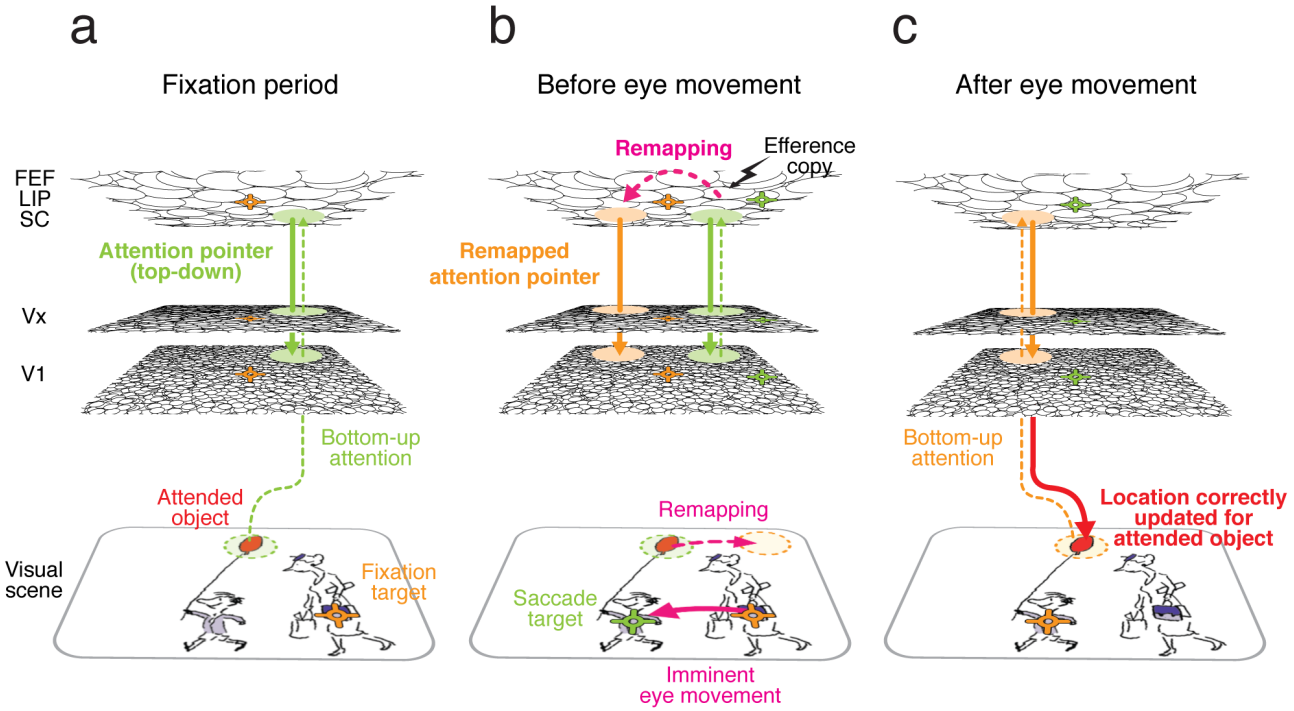


Figure 6. Remapping of attention pointers. Visual cortical areas encode on retinotopic maps different features of the visual scene. Spatial location is coded relative to fixation (the fovea), such that objects to the left of fixation fall on the right part of each area and vice versa. (a) At fixation, visuo-motor attention maps (e.g. LIP, FEF, SC) receive bottom-up information from an object of interest (attended object) and create a target-related activity peak (attention pointer) that drives top-down signals back through the different visual areas conferring performance benefits. (b) Before the eye movement, an efference copy guides remapping of the position of the attention pointers on the visuo-motor attention maps. (c) Then after the saccade, the attention pointer is already at the new retinal location of the attended object. This remapping of attention pointers allows rapid access to object features co-located at the object's retinal position, as well as the maintenance of a link to the appropriate spatial location for attended objects.

This model of remapping allows the recovery of attended target location across eye and head movements, and leads to the following predictions and questions:

- If the visuo-motor centers serve as location maps for attended targets, they must overcome the problem that comes with the retinotopic representations found in these areas. Specifically, every eye or head movement will shift the retinal location of the pointers out of register with their target's spatial location. However, the remapping of the attention pointers acts to correct these misalignments. This leads us to three predictions that are tested in the first three studies of this thesis: 1) Remapping maintains accurate position judgments of attended targets in spatial coordinates – even if the target has moved elsewhere at the same time as the saccade (motion or displacement judgments). 2) Since remapping is piecemeal, using local correction

for individual targets (Quaia et al., 1998; Wurtz, 2008), it allows for the possibility that that the accuracy of these corrections is different for different retinal locations of saccades, or targets. 3) Since remapping is a dynamic process (Kusunoki & Goldberg, 2003; Nakamura & Colby, 2002), it should be possible to directly visualize it as it occurs using a sufficiently salient stimulus in continuous motion.

- What happens to the location representation (attention pointer) for an attended target when the head moves? Even though the model was not initially made to explain space constancy for head movements, the displacement of retinal objects across head movements could be corrected by attentional remapping if head movement signals are allowed to reposition activity on attention/saccade maps in the same way that eye movement signals do. This addition to the model will be tested with head roll and head translation made across the presentation of two visual probes in the third study of this thesis.

- Next, remapping transfers activity from one location to its expected post-saccadic location. What are the spatial limits of this transfer? Can remapping transfer a representation to a location outside the visual field? Neither the model nor the physiological description of remapping make any prediction here since it is commonly assumed that retinotopic, visuo-motor areas are limited to the representation of the visual field. Nevertheless, a test of apparent motion across a saccade allows us in our fourth study to examine whether visual cortices may also register extra-retinal locations.

- Finally, remapping should be in the direction opposite to the eye movement. This however is controversial (Mathôt & Theeuwes, 2010). In what direction do attention pointers really move? Also, what happens to the attention that was at the retinal location of the target just before the saccade? Physiology suggests that activity can be seen at both the pre- and post-saccadic locations (Kusunoki & Goldberg, 2003). In a fifth study we use a behavioral measure of attentional benefits drawn to a transient cue to evaluate the allocation of attention around the time of a saccade. The remapping of attention should start just before the onset of the saccade, shifting attention on the retinotopic representation away from the cue such that after the saccade, it will be shifted back onto the correct location in space. Such predictions as well as side effects of trans-saccadic attention cueing (the retinotopic trace of attention, Golomb et al., 2008) will be evaluated both before and after the saccade in the last study of this thesis.

4. Experiments

4.1 How can we evaluate remapping accuracy?

4.1.1. Objectives and summary of results

In this first study we showed that remapping — the correction of a target location for the effects of eye movements – could be evaluated in a non-invasive fashion using moving targets. We examined what happens when an attended target moves at the time of the saccade. In particular, we presented a probe in one location just before the saccade and then at a second location just after the saccade. Because of the intervening saccade, the displacement between the two locations on the retina was very different from the displacement in the world. Normally, we see objects moving only when they actually move in the world and not whenever our eyes move; our visual system corrects for eye movements. However, here we are asking what happens if something moves at the same time as our eyes move. Change blindness (Grimes, 1996; Henderson & Hollingworth, 1999) demonstrates that we are unable to see displacements that occur at the time of a saccade, unless it is the displacement of an attended item (O'Regan et al., 1999). Even then, if an attended target is displaced along the direction of the saccade and the target is present when the saccade lands, significant shifts may still go undetected (Bridgeman et al., 1975). Nevertheless, under some conditions, shifts at the time of the saccade are seen: for large displacements (Bridgeman et al., 1975), displacements orthogonal to the saccade (Niemeier, Crawford, & Tweed, 2003), and displacements where the target reappears after the saccade has landed (Deubel et al., 1996). In the present experiments, we used a stimulus that had all three of these properties, maximizing the visibility of the trans-saccadic motion.

In the first two of our four experiments here, we tested vertical probe displacements of 3° of visual angle, orthogonal to the horizontal saccade of 10°, allowing us to examine the accuracy of the compensation for the eye movements at 9 different locations across the visual field. Any local variation in the accuracy of the corrections should help differentiate among possible mechanisms of space constancy (as discussed in the introduction to the thesis). In the first experiment, we asked observers to adjust the relative horizontal offset between the pre- and post- saccadic dot locations until the two dots appeared vertically aligned. Deviations from vertical alignment on the screen were taken to characterize deviations from accurate correction of the saccade. From these measurements, we constructed a map of correction errors for different attended locations within 15° of the fovea. The second experiment studied the same trans-saccadic apparent motion but this time using the method of constant stimuli in conjunction with eye movement tracking. The third and fourth experiments were controls that measured perceptual biases in judgments of position and orientation in the absence of saccades to determine if these factors had influenced our results in the first two experiments.

We demonstrate in our two first experiments that vertical motion straddling a horizontal saccade was seen in spatial coordinates. There was, nonetheless, some deviation between the perceived motion and the actual motion as it occurs in space, suggesting that biases in the correction represent about 5% of the saccade length. These deviations varied significantly across locations in the visual field.

We also observed variations in these local biases across participants. These idiosyncratic patterns were stable over test–retest intervals of up to 3 months. The second experiment showed that these errors held up when measured using a different method (constant stimuli instead of adjustment) and after sorting trials to limit the analysis to trials where the saccade occurred between the presentation of the two positions of the apparent motion stimulus. Additionally, in two control experiments we found that local biases in judging verticality had little or no effect whereas the position biases could account for about a quarter of the amplitude of the local biases in saccade correction.

Of most interest was our observation of local variation in the correction for the saccades, a result that argues against global approaches to space constancy (see the introduction to the thesis). Our results support local correction mechanisms like the remapping process seen in single cell activity on saccade centers (Wurtz, 2008). The correction in this remapping case is applied to individual attended targets (Rolfs et al., 2011), and even though the same efference copy vector drives the correction for each target, the conversion of the vector to a shift on the roughly log polar coordinates of the saccade control maps is idiosyncratic for each location and direction (Cavanagh et al., 2010).

Using an apparent motion test, we demonstrate that trans-saccadic displacement is perceived in roughly spatial rather than retinal coordinates. This spatiotopic apparent motion provides a simple method for measuring the accuracy of the processes that correct for eye movements and shows that there is significant local variation in the correction process. These local variations suggest that space constancy depends on local corrections consistent with the physiological remapping of individual attended targets, supporting our model of a remapping of attention pointers.

Spatiotopic apparent motion reveals local variations in space constancy

Martin Szinte

Centre Attention and Vision,
Laboratoire Psychologie de la Perception,
Université Paris Descartes, Paris, France, &
CNRS UMR 8158, Paris, France

Patrick Cavanagh

Centre Attention and Vision,
Laboratoire Psychologie de la Perception,
Université Paris Descartes, Paris, France, &
CNRS UMR 8158, Paris, France

While participants made 10° horizontal saccades, two dots were presented, one before and one after the saccade. Each dot was presented for 400 ms, the first turned off about 100 ms before, while the second turned on about 100 ms after the saccade. The two dots were separated vertically by 3°, but because of the intervening eye movement, they were also separated horizontally on the retina by an additional 10°. Participants nevertheless reported that the perceived motion was much more vertical than horizontal, suggesting that the trans-saccadic displacement was corrected, at least to some extent, for the retinal displacement caused by the eye movement. The corrections were not exact, however, showing significant biases that corresponded to about 5% of the saccade amplitude. The perceived motion between the probes was tested at 9 different locations and the biases, the deviations from accurate correction, varied significantly across locations. Two control experiments for judgments of position and of verticality of motion without eye movement confirmed that these biases are specific to the correction for the saccade. The local variations in the correction for saccades are consistent with physiological "remapping" proposals for space constancy that individually correct only a few attended targets but are not consistent with global mechanisms that predict the same correction at all locations.

Keywords: saccade, remapping, spatial vision, space constancy, motion, visual cognition

Citation: Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision, 11*(2):4, 1–20, http://www.journalofvision.org/content/11/2/4, doi:10.1167/11.2.4.

General introduction

In this paper, we examine what happens when an attended target moves at the time of the saccade. Does saccadic suppression (Matin, 1974; Volkmann, 1986) make the displacement invisible (Bridgeman, Hendry, & Stark, 1975)? Otherwise, if we do see the motion, is it determined by the displacement on the retina (retinotopic displacement) or by the displacement in space (spatiotopic displacement)? If the perceived motion is determined by displacement in space, how are the perceived locations corrected for the effects of the eye movements on retinal input? We address these questions with an apparent motion display, where, in its standard version, a salient stimulus is briefly presented at one location and then reappears at a different location, leading to a strong impression of motion. To use apparent motion in the context of saccades, we present the stimulus at its initial location just before the saccade and then present it at a second location just after the saccade. Because of the intervening saccade, the displacement between the two locations on the retina is very different from the displacement in the world (Figure 1). Motion during a saccade, whether of the saccade goal itself (e.g., Bridgeman et al., 1975) or the whole visual scene (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; McConkie & Currie, 1996), is strongly suppressed. Despite this suppression, a displacement can be seen if it is quite large (1/3 of the saccade amplitude or more, Bridgeman et al., 1975) or if it is orthogonal to the saccade (Niemeier, Crawford, & Tweed, 2003, although see also Bridgeman et al., 1975) or if the displaced probe is not present when the saccade lands but is turned on at least 50 ms after the saccade lands (Deubel, Schneider, & Bridgeman, 1996). In our experiment, we wanted to maximize the chance of seeing motion, so our stimuli had all three of these properties.

Rock and Ebenholtz (1962) were the first to test the perception of apparent motion across saccades using displacements that were the same magnitude as the saccade. In this case, both pre- and post-saccadic targets fell on the same retinal location, the fovea, but despite this absence of retinal displacement, participants reported that motion was seen. This earlier finding was supported by the recent report that more complex transformational apparent motion could be seen across saccades (Fracasso,

doi: 10.1167/11.2.4 Received August 14, 2010; published February 4, 2011 ISSN 1534-7362

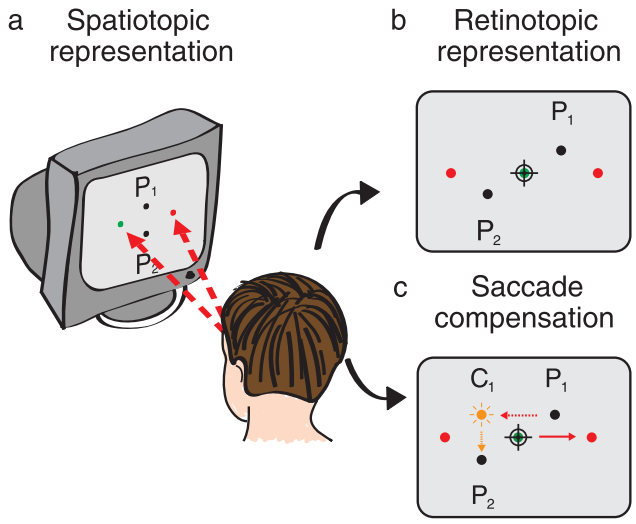


Figure 1. Compensation for saccades. (a) Participants were instructed to fixate the green dot that exchanged position with a red dot each 600 ms. While they were fixating to the left, the first black probe (P_1) appeared for 400 ms; they then saccaded to the right and a second probe (P_2) of the same duration appeared below the first one 200 ms after the offset of P_1. (b) On the retina, the first probe falls to the right side of the fovea while the second falls to the left side. (c) To compensate for these effects of the saccade, the visual system corrects the expected location of P_1 in the opposite direction to the saccade (red dashed arrow) to obtain C_1. If this correction is accurate, motion is perceived in its spatiotopic (vertical motion: from C_1 to P_2) rather than retinotopic direction (oblique motion: from P_1 to P_2) and space constancy is maintained.

Caramazza, & Melcher, 2010). The authors of both studies concluded that apparent motion was seen between locations in space not locations on the retina although they did not test how well the perceived motion matched the actual trajectory in space. Nevertheless, the first stimulus location must have been corrected to some extent to compensate for the eye movement, rendering an impression of motion despite the absence of motion on the retina. For our stimulus, we expect that motion will be seen, as Fracasso et al. (2010) and Rock and Ebenholtz (1962), principally in spatial, not retinal, coordinates. We are interested in whether there are any systematic deviations from spatial coordinates, from accurate compensation for eye movements. In particular, we tested vertical apparent motion at 9 different locations across the visual field to determine whether the deviations from accurate correction, if any, varied as a function of location. Any local variation in the accuracy of the corrections should help differentiate among possible mechanisms of space constancy.

What are the possible mechanisms of space constancy? We make a rough division between global correction approaches and local corrections for eye movements. For global corrections, some decision about visual stability or some overall correction or calibration is determined and applied uniformly to the visual input (see Bridgeman, Van der Heijden, & Velichkovsky, 1994 for a review). As Bridgeman (2007) and Bridgeman et al. (1994) point out, there are a number of possible corrective mechanisms. For example:

1. Shift and compare. A copy of the motor commands to the eyes, efference copy or corollary discharge, is used to predict the retinal input following the saccade, and if there is a match to new input, it assumed that the world has been stable (e.g., Sperry, 1950; von Holst & Mittelstaedt, 1950). This has been amended to allow for some degree of mismatch before stability is rejected (Bridgeman et al., 1975).
2. Spatiotopic maps: The efference copy is used to transfer retinal input onto a map in spatial coordinates (e.g., Bischof & Kramer, 1968; Breitmeyer, Kropfl, & Julesz, 1982).
3. Reference object calibration. A memory of the saccade target "landscape" (the target and possibly a few attended items, especially those near the target; Irwin, McConkie, Carlson-Radvansky, & Currie, 1994) is used to locate the original saccade goal (e.g., Bridgeman et al., 1994; Deubel, Bridgeman, & Schneider, 1998; Deubel, Koch, & Bridgeman, 2010; Koch & Deubel, 2007). The rediscovered target then serves as a reference for spatial localization providing space constancy without using the efference copy.

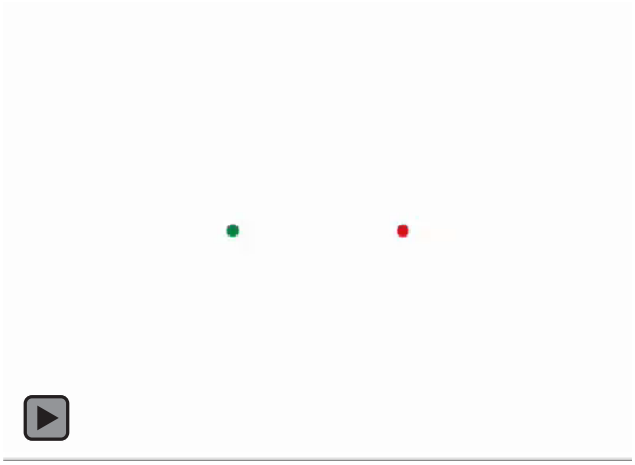
In all these cases (with various caveats, see Bridgeman, 2007; Bridgeman et al., 1994), once the correction is determined, it would be assumed to hold across all locations. The eye movement is, after all, a shift of the whole visual image by the same vector and a uniform correction (e.g., Honda, 1989; Matin & Pearce, 1965) would be reasonable (ignoring deviations due to optical aberrations and the spherical retina).

As an alternative to these global approaches, physiological studies have suggested a piecemeal compensation where corrections, based on efference copy (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990; Sommer & Wurtz, 2004, 2006; Wurtz, 2008), are applied to the representations of only a few attended items on the retinotopic maps of saccade control centers (Gottlieb, Kusunoki, & Goldberg, 1998; Kusunoki, Gottlieb, & Goldberg, 2000). This shift of activity for each target to its expected post-saccadic location, called "remapping," starts before the target lands and is seen even if the target is removed during or even before the saccade and so never lands there (Duhamel et al., 1992; Umeno & Goldberg, 2001). The remapping produces a crude spatiotopy for attended items (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), and if it

actually underlies the space constancy we experience, then displacements of any unattended items should not be seen (widely reported as the change blindness phenomenon; Cavanaugh & Wurtz, 2004; O'Regan, Rensink, & Clark, 1999; Rensink, O'Regan, & Clark, 1997). Critically, this blindness occurs only for non-attended items (Rensink et al., 1997). The correction in this "remapping" proposal is applied to individual attended targets, and so, unlike global correction schemes, there is no assumption that the correction be the same everywhere. It is the same efference copy vector that drives the correction for each target, but the conversion of the vector to a shift on the roughly log polar coordinates of the saccade control maps is idiosyncratic to each location and direction. Indeed, in two models of this process (Keith & Crawford, 2008; Quaia, Optican, & Goldberg, 1998), the link between the target location and the saccade vector that predicts the post-saccadic location must be learned independently for each location and saccade. Location-specific mislocalizations are a general property of peri-saccadic position judgments (Honda, 1989; Matin & Pearce, 1965) and specifically of the compression effects seen around the time of the saccade (Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). If these effects are related to the updating of locations required for spatial constancy, they are most likely the intermediate results of shifting of coordinates rather than the final values of correction that interest us here. Nevertheless, we will compare any local variations in position judgments that we find here with those found in peri-saccadic mislocalization experiments.

In our experiments, we test vertical displacements of 3° of visual angle, orthogonal to the horizontal saccade of 10°, allowing us to examine the accuracy of the compensation for the eye movements as a function of location. The current study contains four experiments. In the first experiment, we asked participants to adjust the relative horizontal offset between the pre- and post-saccadic dot locations until the two dots appeared vertically aligned. A demonstration of the stimulus is shown in Movie 1. Deviations from vertical alignment on the screen were taken to characterize deviations from accurate correction. From these measurements, we construct a map of correction errors for different attended locations within 15° of the fovea. The second experiment studied the same trans-saccadic apparent motion but this time using the method of constant stimuli in conjunction with eye movement tracking. The third and fourth experiments are controls that measured perceptual biases in judging position and orientation in the absence of saccades to determine if these factors had influenced our results in the first two experiments.

We find, as Rock and Ebenholtz (1962) and Fracasso et al. (2010) did, that apparent motion is not seen in retinal coordinates. However, the tilt of the direction of apparent motion away from vertical that is visible to most observers in our demonstration movie (Movie 1) and reported by all our participants indicates that the correction for eye movements does not correspond to exact space constancy. The errors are on the order of 5% of the saccade amplitude and are quite noticeable as tilts away from vertical of up to about 9° of rotation. More important, these errors vary systematically as a function of the location of the stimuli in the visual field suggesting that the compensation for eye movements is not a uniform, global process. The control experiments show that these are errors intrinsic to the correction process and are not biases in position or motion verticality judgments in the absence of eye movements. Because of the timing we used in presenting the first and second stimuli (duration of 400 ms, separated by 200 ms), we believe that these errors reflect the final, stable product of correction independently of the brief mislocalizations that occur around the time of the eye movement as the correction is in progress (Honda, 1989; Matin & Pearce, 1965). Indeed, the patterns of errors we see in our results are inconsistent with and often opposite to the displacements toward the saccade target seen for peri-saccadic compression effects.



Movie 1. Stimulus demonstration.

Experiment 1

Introduction

In order to test whether trans-saccadic motion is seen in retinotopic or spatiotopic coordinates, we asked participants to adjust the horizontal position of two dots displayed sequentially one before and one after the saccade until they appeared vertically aligned (Figure 2). If motion were experienced retinotopically, the dots would have to be shifted horizontally by 10° (the size of the saccade) to appear aligned. If the motion were experienced

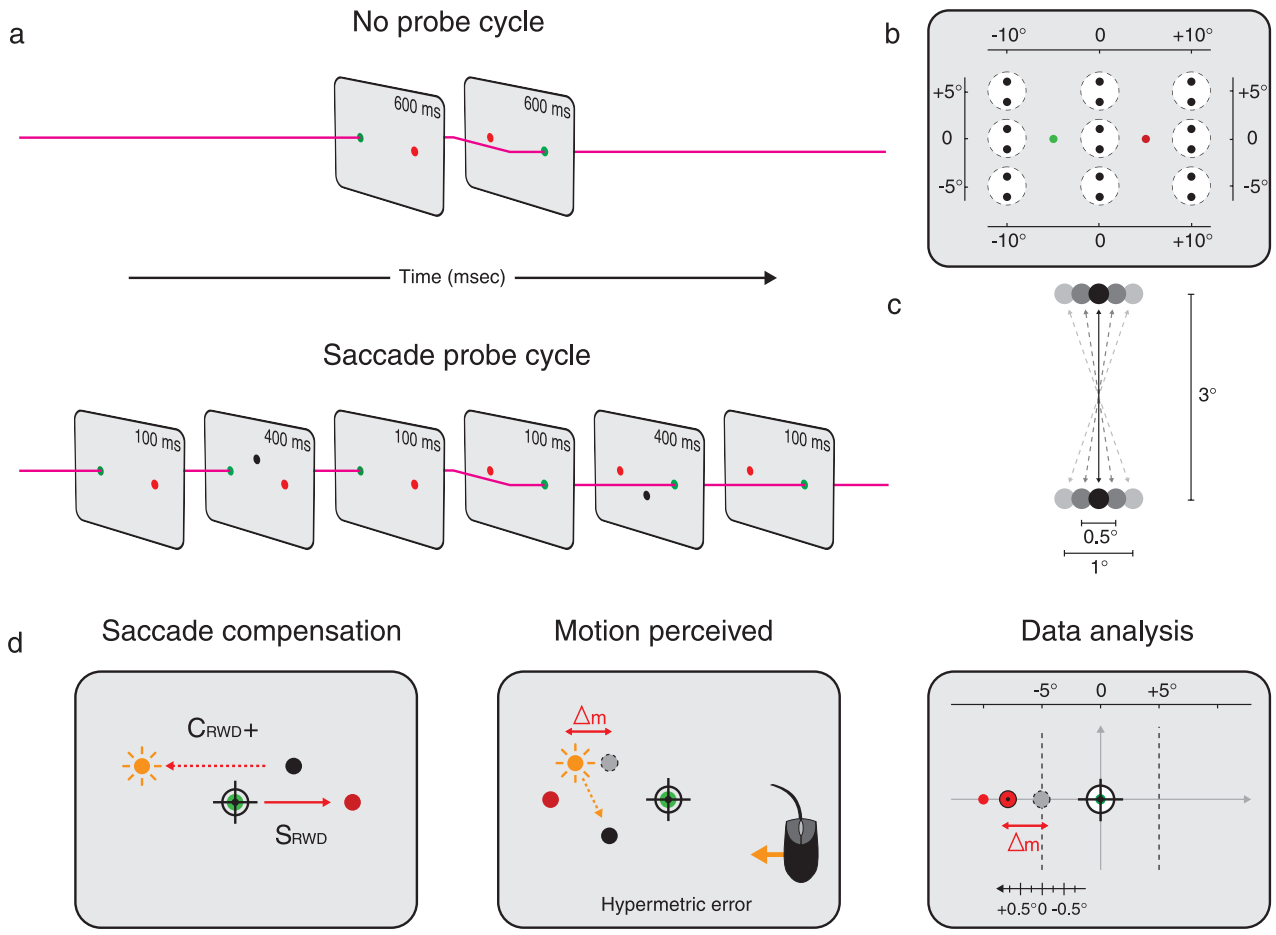


Figure 2. Stimuli sequences, probe locations, and data analysis. (a) Spatial layout of the stimuli for a rightward saccade trial. The magenta line represents the line of gaze during each cycle. Participants were instructed to saccade to the green dot as it exchanged locations with the red dot each 600 ms while no probes were presented. In the "saccade probe cycle," participants continued to saccade to the green dot as it changed positions, but now black probe dots were presented before and after the saccade either top-first or bottom-first (only top-first is shown here). (b) The pairs of probes could appear at 9 different spatial locations equally spaced by 10° horizontally and 5° vertically. (c) In Experiment 1, participants used a mouse to adjust the horizontal location of the probes, which were originally displaced vertically by 3° but could be displaced horizontally by ±0.5° or ±1° producing an initial random left or right physical tilt. (d) To compensate for the effect of the saccade, the visual system corrects the expected location of the first black probe in the opposite direction to the saccade (red dashed arrow). The correction vector (C_{RWD}) could be either too long (hypermetric error, displayed here) or too short (hypometric error, not displayed) reflecting, respectively, an over- or undercompensation of the saccade vector (S_{RWD}). After the saccade (middle panel), this error leads to the perception of a tilted motion from the corrected location of the first probe (orange dot) to the second probe location. Participants adjust the two dot locations until the perceived motion is vertical. The error of correction (right panel), that is, the difference between the top and bottom probe horizontal positions ("Δ_m"), is measured and displayed (red dot) at each tested location (top scale), as an offset relative to the accurate correction for the saccade (gray dashed dot). The bottom scale represents the direction (positive as hypermetric, negative as hypometric error) and the amount of the error.

spatiotopically, the two dots would appear to move vertically when they were aligned vertically in the display screen. If there were any inaccuracies in the correction for the saccade, then the required alignment may be shifted left or right of vertical. We tested this alignment required for perceived verticality at 9 different positions in the visual field.

Methods

Participants

Four volunteers from the Université Paris Descartes took part in the first experiment (2 authors and 2 participants naive to the purpose of the experiment, age 23–61 years; 1 female). All had normal or corrected-to-

Movie 2. Stimulus used during a rightward saccade-downward motion trial of the Experiment 1 and 2.

normal vision and gave their informed consent. Experiments were carried out according to the ethical standards specified in the Declaration of Helsinki.

Stimuli

Participants were seated in a silent and dimly lit room with the head positioned on a chin rest, 63 cm in front of a computer screen. Stimuli were red, green, and black 0.7° diameter dots on a gray background, presented on a 22″ Formac ProNitron 22800 screen with a spatial resolution of 1440 by 1050 pixels (or 36.7° by 27.6°) and a vertical refresh rate of 100 Hz. The experiment was controlled by an Apple MacPro Dual Intel-Core Xeon computer. Manual responses were acquired via a standard keyboard and mouse. The experimental software controlling stimulus display and response collection was implemented in Matlab (MathWorks, Natick, MA), using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Procedure

Two dots, one green and one red, were presented at 5° to the right and 5° to the left of screen center. The red and green dots exchanged position each 600 ms. Participants were instructed to always fixate the green dot and follow it as accurately as possible as it moved back and forth. After a few back and forth cycles with no probes presented, participants were able to synchronize their saccades with the exchange of the two fixation dots ("no probe cycle" in Figure 2a). Once they judged that they were moving their eyes in synchrony with the green dot, they were instructed to press a button on the keyboard to start a trial. As they pressed the button, two circular black probes were presented sequentially, one before and one after the saccade ("saccade probe cycle" in Figure 2a). Each probe was presented for 400 ms, with a gap of 200 ms between them. If the participant's eye movements were synchronized to the exchange of red and green fixation dots, the first probe would be turned off about 100 ms before the saccade and the second turned on about 100 ms after the saccade. These assumed timings were not verified in this experiment but were in Experiment 2. Each "saccade probe cycle" was alternated with a "no probe cycle," allowing the equiprobable presentation of probes during leftward or rightward saccade trials (see Movies 2 and 3). These probes could appear at nine equiprobable locations on the screen equally spaced by 10° horizontally and 5° vertically from center of the screen (Figure 2b). The first black probe is originally displaced vertically by 3° from the second probe, but this displacement could be one of four other combinations of horizontal shifts of the two probes by ±0.5° or ±1.0°, producing a left or right physical tilt (Figure 2c), randomizing the initial tilt of the probes across trials. Finally, the order of appearance of these two probes was equiprobably top-first or bottom-first, producing equal numbers of upward or downward displacement trials.

As they moved their eyes back and forth, participants were instructed to use the computer mouse to adjust the horizontal position of the two probes (simultaneously in an opposite direction, the bottom probe in the direction of the mouse and the top probe in the opposite direction) until they perceived motion between them to be vertical. Once participants were satisfied with the adjustment, they pressed a button to indicate their final setting and another trial began. Three participants ran 5 blocks of 36 trials each (180 trials) and one participant ran 6 blocks (216 trials). Moreover, to determine the stability across time of the observed effect, two participants ran the same 5 blocks (180 trials) and 6 blocks (216 trials) a second time, after a 3-month delay.

Movie 3. Stimulus used during a rightward saccade-upward motion trial of the Experiment 1 and 2.

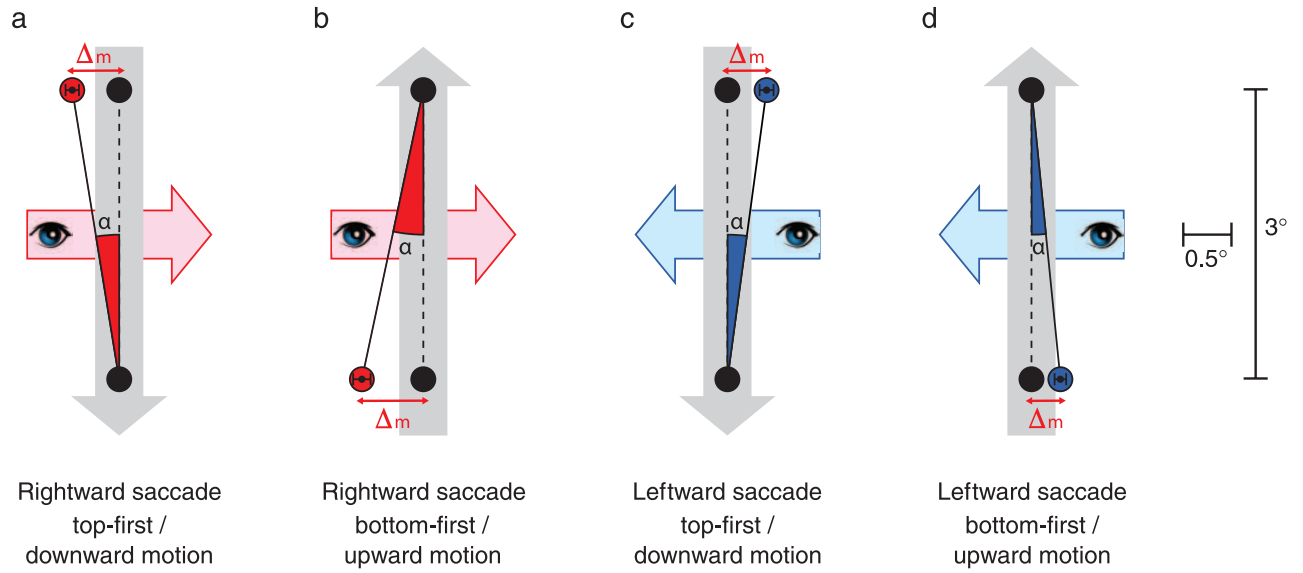


Figure 3. Combinations of saccade and motion directions. In each panel, the colored arrow shows the direction of the saccade and the gray arrows show the direction of the motion. The red and blue dots represent the recovered or corrected location of the first probe relative to the second for all participants and for the central probe presentation (error bar indicates *SEM*). In all these cases, the error observed was an overcompensation of the saccade vector: the recovered location of the first probe is displaced beyond its actual spatial location in the direction opposite to the saccade. To characterize these correction errors, we first use the horizontal shift the subjects add to the display ("Δ_m") in order to make it appear vertical. We then correct the sign of the "Δ_m" each time for the saccade direction and motion direction to recover whether the error was a hypermetric correction (as shown here) or a hypometric correction. For downward motion and rightward saccades (a), this overcompensation of the saccade vector produces a clockwise rotation of the perceived direction, as it does for the leftward saccade and upward motion (d). When we combine alternating left and right saccades with alternating up and down motions as we do in demonstration Movie 1 (either (a) and (d), or (b) and (c)), the tilt will therefore appear the same on each saccade. In the experiment, we test only one combination of saccade and motion direction at a time (see Movies 2 and 3, respectively, for the conditions of (a) and (b)).

Results

Participants adjusted the horizontal positions of the probes to make their displacement appear vertical. If the compensation for saccades is accurate, the final setting will be accurate on the screen. If compensation is not perfect, however, the adjustment, "Δ_m," away from actual vertical measures the over- or undercompensation of the saccade vector (hypermetric or hypometric correction). We analyzed four sets of nine mean adjustments arising from the combination of the two directions of saccades (rightward and leftward) with the two directions of the probes (bottom-first and top-first). Figure 3 shows the different combination of the directions of saccade and directions of motion with the adjustment observed across participants for probes presented centrally. For this specific position, we always observed overcompensation of the saccade vector leading for specific combination of variable to clockwise (Figures 3a and 3d) or counter-clockwise perceived motion (Figures 3b and 3c), when probes are vertically aligned on the screen. We then correct the sign of the "Δ_m" each time for the saccade direction and motion direction to recover whether the error was a hypermetric correction or a hypometric correction.

We tested rightward and leftward saccades independently and rather than combining their data, we treated them as 18 different test locations as we were interested in the correction for eye movements at all 18 retinal locations of the first probe, the one appearing before the saccade. We then ran an ANOVA for these eighteen retinal positions with the two directions of the probes (downward vs. upward) as independent variables and with the data reversion explained above. The ANOVA showed a strong main effect of the different retinal positions on the perceived vertical alignment ($F(17, 51) = 4.26$, $p < 0.001$). However, there was no significant difference of perceived alignment for downward vs. upward displacement ($F(1, 51) = 0.03$, $p > 0.85$) nor an interaction of this variable with the retinal positions of the probes ($F(17, 51) =$ 1,26, $p > 0.25$). We thus collapsed the data across upward vs. downward displacement in all further analyses and in the data figures.

Group and individual data are shown in Figures 4 and 5, respectively. Results are presented in retinal coordinates (i.e., in coordinates relative to the fovea) and are

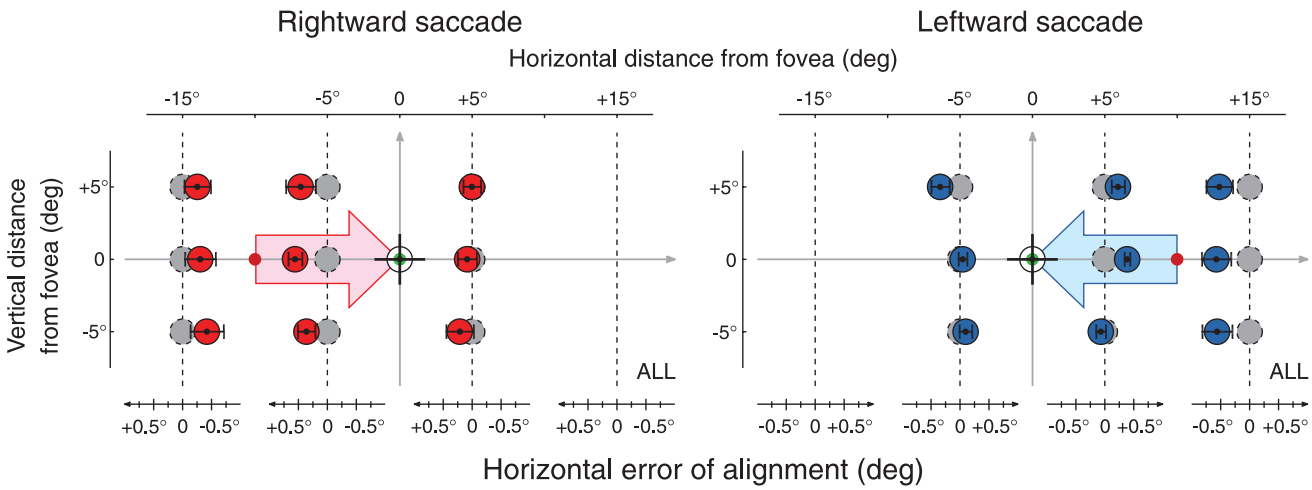


Figure 4. Horizontal error of alignment derived from the adjustments required to make the motion between the two probes appear vertical. The data are averaged across the 4 participants and shown separately for rightward and leftward saccades at each of the 9 tested locations. The gray dots show horizontal locations where the first stimulus should be perceived to support accurate vertical motion in world coordinates. Data are presented in retinal coordinates with the central cross showing the location of the fovea, following the saccade. The small red and green dots indicate the fixation and saccade target. Scales at the top and at the left of each map reflect the horizontal and vertical distances from the fovea tested with each of 9 probe pairs. The scale below each map gives the mean value of alignment errors for each spatial location tested. Note that these scales are reversed for rightward and leftward saccades, with positive values always representing overcompensation or hypermetric correction and negative values representing undercompensation or hypometric correction. The alignment scales are also magnified by a factor four relative to the retinal scale to make these deviations clearly visible. Horizontal error bars indicate *SEM*.

plotted on maps of horizontal error of alignment as a function of saccade direction. Each graph shows, for the nine retinal locations tested during leftward and the nine tested during rightward saccades, the accurately corrected location of the first probe that would support space constancy in gray (gray dashed dots in Figures 4 and 5) and the horizontal deviation from that location (red and blue dots in Figures 4 and 5) corresponding to the horizontal distance between the two probes ("Δ_m") after the participant's adjustment. Group results indicate that the corrected location of the first probe was significantly over- or underestimated by different amounts depending on its location.

As expected from the Rock and Ebenholtz (1962) and Fracasso et al. (2010) results, the group and individual data for all retinal locations tested suggest that the direction of apparent motion between the two probes is perceived more in world coordinates than in retinal coordinates. For example, for the presentation of an apparent motion at the vertical and horizontal center of the screen in the case of a rightward saccade (see coordinates [0°, −5°] in rightward map in Figure 4), we observed a hypermetric correction of 0.55° ± 0.13° (an overcompensation). This perceived misalignment of about one-half a degree is about 5% of the 10° shift of the probes' projections on the retina. The magnitudes of the correction errors are shown in Figure 6 and indicate that across participants, a 10-deg saccade leads to less than 4% (0.38° ± 0.09° deg for 10-deg saccade) of errors from exact space constancy for targets presented within 15° of the fovea. These variations from accurate correction of the saccade vary significantly ($p < 0.001$) across the 9 locations and two directions of saccades. Note that, if the motion had been seen in retinal coordinates, the correction would have been an offset of 10° of visual angle and the rotation from vertical, the apparent direction of motion, would have been 73°, much closer to horizontal (at 90°) than vertical (at 0°). Thus, this first experiment demonstrated that participants perceived the probe displacement in roughly spatiotopic rather retinotopic coordinates and that the correction for the eye movements has a small but significant error that depends on location.

The variation in vertical alignment averaged across participants explained about 40% of the total within-participant variance and we next analyzed the direction and the magnitude of the local correction biases for each participant. Figure 5 shows the intersubject variability in the amount and the direction of biases between locations tested and saccade directions. For probes where the correction crosses the vertical midline, the correction errors were hypermetric in all participants (data in horizontal coordinates −5° on the rightward maps and +5° on the leftward maps in Figure 5). However, when the correction for the eye movement left the probe in the same hemifield, the pattern of local biases varied substantially

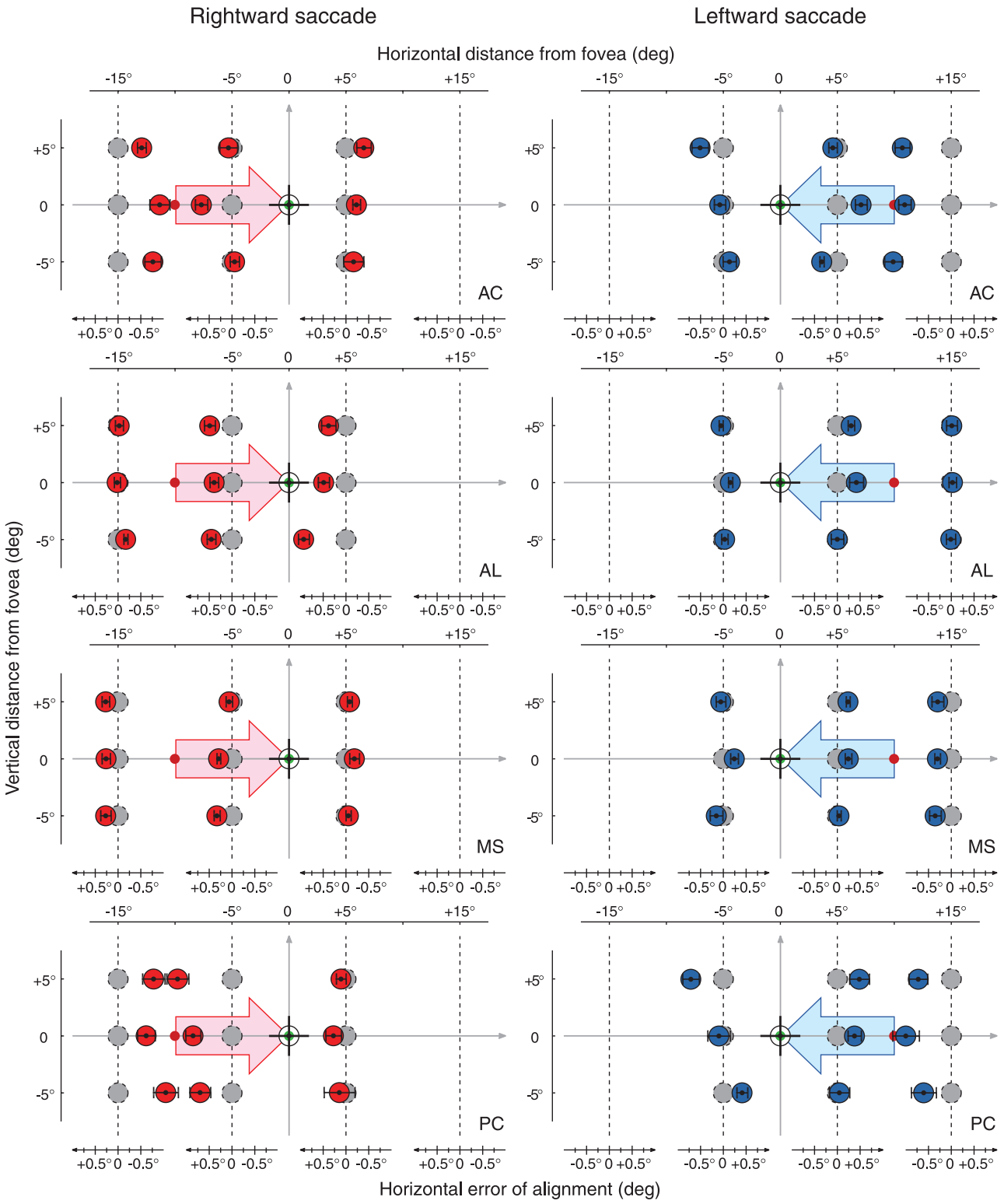


Figure 5. Individual results. Each row corresponds to rightward and leftward saccade trials for each participant. Conventions used here are described in Figure 4.

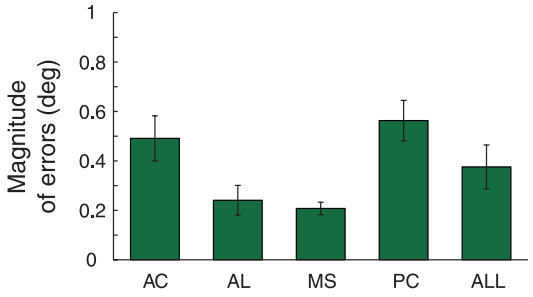


Figure 6. Magnitude of correction errors for individuals and group. Each bar represents the mean values of alignment bias independently of the sign of the effect (absolute value) averaged over the nine spatial locations and two saccade directions. Error bars indicate *SEM*.

from participant to participant (data in horizontal coordinates −15° and +5° in rightward maps; −5° and +15° in leftward maps in Figure 5).

This variability was not just measurement noise as the individual patterns showed significant intertrial reliability. In particular, two participants were tested two times with 3 months between the two sessions. The horizontal errors of alignments observed for each of the nine spatial locations tested twice were between each other similar and highly correlated (AC: $R^2 = 0.72$, one-tailed t-test, $p < 0.001$; MS: $R^2 = 0.86$, one-tailed t-test, $p < 0.001$) across this large interval, demonstrating the robustness of the individual patterns.

Finally, from the group and individual data, there is a tendency for first probe location to appear displaced toward the fixation target (red dots in Figures 4 and 5). Unlike the very large peri-saccadic compression effects (e.g., Ross et al., 1997, often equal to the saccade amplitude), this compression effect is centered on the initial fixation not the saccade target and is much smaller (about 5% of the saccade amplitude). It is observed on group results for both directions of saccade (see Figure 4) and is more or less pronounced for each participant (see Figure 5).

Discussion

The results of Experiment 1 show that trans-saccadic, vertical, apparent motion is seen in a roughly spatiotopic rather that a retinotopic reference frame, consistent with previous results (Fracasso et al., 2010; Rock & Ebenholtz, 1962) and extending it beyond Rock and Ebenholtz's conditions to motion orthogonal to the saccade direction at location other than saccade target. These results suggest that the location of a pre-saccadic, attended target has been corrected for the saccade so that when the target then reappears in a new location, its displacement from the first location is seen roughly in world coordinates. The salience of the motion direction allowed us to measure deviations from world coordinates quite accurately, deviations that we attribute to significant ($F(17, 51) = 4.26$, $p < 0.001$) local biases in correction. When programming a 10-deg saccade, attended targets within 15° of the fovea are corrected to their post-saccadic retinal locations with errors representing less than 4% of the saccade amplitude. Moreover, beyond the local variation in the correction errors common to all participants, we also observed local biases specific to each that were quite stable across as much as a 3-month interval.

Experiment 2

Introduction

The results of the first experiment clearly suggest that trans-saccadic motion is seen in roughly spatiotopic rather than retinotopic coordinates. However, because we did not measure eye movements, one might argue that participants made saccades too early or too late and had an opportunity to see the two probes during a single fixation. In this second experiment, we used a method of constant stimuli with the trans-saccadic apparent motion of the first experiment and then analyzed only those trials with appropriate eye movements. We restricted the tested locations to only the three along the horizontal midline rather than all 9 tested in Experiment 1, but again for both leftward and rightward saccades. This procedure allows us to determine first whether the observed motion remains roughly spatiotopic on trials when the eye movement intervenes between the first and second stimuli and, second, whether the observed direction of motion is affected by the position of each saccade landing.

Methods

Participants

Two participants from first experiment took part in the second experiment (1 author and 1 participant, age 24–25 years).

Instruments and stimuli

Participants were seated in a quiet and dimly lit room with the head positioned on a chin rest, 63 cm in front of a computer screen. Stimuli, display, and computer configurations were identical to those in the first experiment. Movements of the right eye were measured using an EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) with a sampling at 1 kHz. The experimental software controlling stimulus display and response collection was implemented in Matlab (MathWorks, Natick, MA), using the Psychophysics (Brainard,

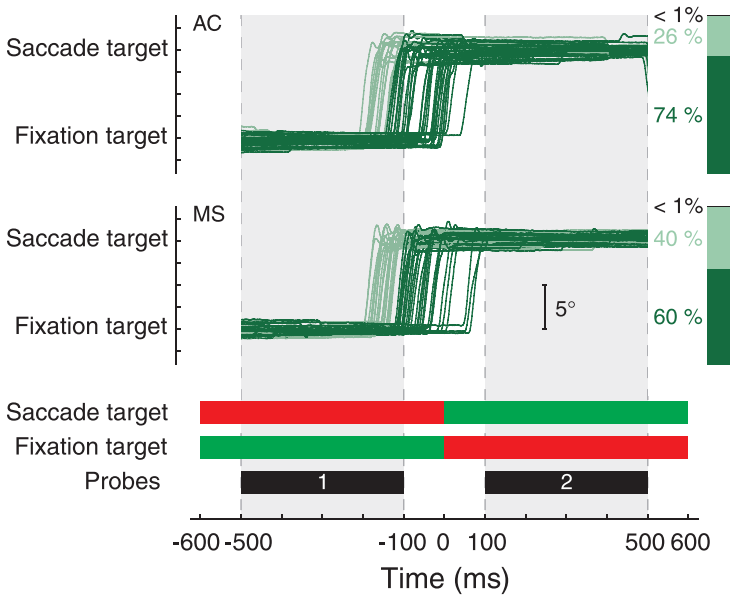


Figure 7. Trial selection. This graph shows fifty representative horizontal eye traces of individual probe cycles for each participant. The bars at the bottom of the figure represent the onset, the offset, and the colors of the saccade target, the fixation target, and the first and second probes. To be sure that apparent motion was tested trans-saccadically, we sorted trials into 3 categories, "early saccade" (light green lines), "late saccade" (black lines, not displayed because they represent less than 1% of trials for both participants), and "correct saccade" trials (dark green lines) where saccades end before the onset of the second probe (see text). Bars at the right of the figure represent the proportion of trials in each category for each participant.

1997; Pelli, 1997) and EyeLink (Cornelissen, Peter, & Palmer, 2002) toolboxes. Manual responses were acquired via a standard keyboard. Saccades were analyzed offline using a two-dimensional velocity space algorithm developed by Engbert and Mergenthaler (2006). Psychometric functions were fitted using the Psignifit toolbox (Wichmann & Hill, 2001a, 2001b).

Procedure

Each trial began with two "no probe cycles" (Figure 2a) in which two dots, one green and one red, swapped positions with the same temporal configuration as in Experiment 1. These two initial sequences help participants to synchronize their saccades with the exchange of the two dots and to prepare themselves for the main sequence. Following these two sequences, a "saccade probe cycle" (Figure 2a) was displayed once. In this third sequence, two black probes were displayed sequentially with one of 11 equiprobable horizontal gaps between them, from −1.75° (bottom probe to the left of the top probe) to +1.75° (bottom probe to the right of the top probe) following a constant stimuli procedure. We tested three horizontal locations of the nine spatial locations used in the first experiment. Thus, probes could appear at three equiprobable locations on the horizontal midline of the screen, equally spaced by 10° from the center of the screen. The overall displacement between the two black probes ranged from 3° (when probes were displayed vertically) to ~3.5° (when probes were horizontally displaced by ±1.75°). Finally, as in Experiment 1, the probes' order of presentation was equiprobably bottom-first (downward motion) or top-first (upward motion).

After the "saccade probe cycle," a tone indicated that participants were to report the tilt of the motion perceived: clockwise or counterclockwise. One participant ran 10 blocks of 132 trials each (1320 trials) and the other ran 12 blocks of 132 trials each (1584 trials). We selected only trials in which correct saccades were detected, that is trials without blinks, starting and ending in an area within a 2° radius circle centered on the fixation target and on the saccade target. This selection left 90.15% of all trials for the first participant (AC: 1190/1320 trials kept) and 96.02% of all trials for the second participant (MS: 1521/1584 trials kept). Each session was composed of 2 or 3 blocks and always lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min.

Results

In addition to the selection based on spatial accuracy and lack of blinks, we also selected trials based on accurate timing. We instructed participants to initiate their saccade

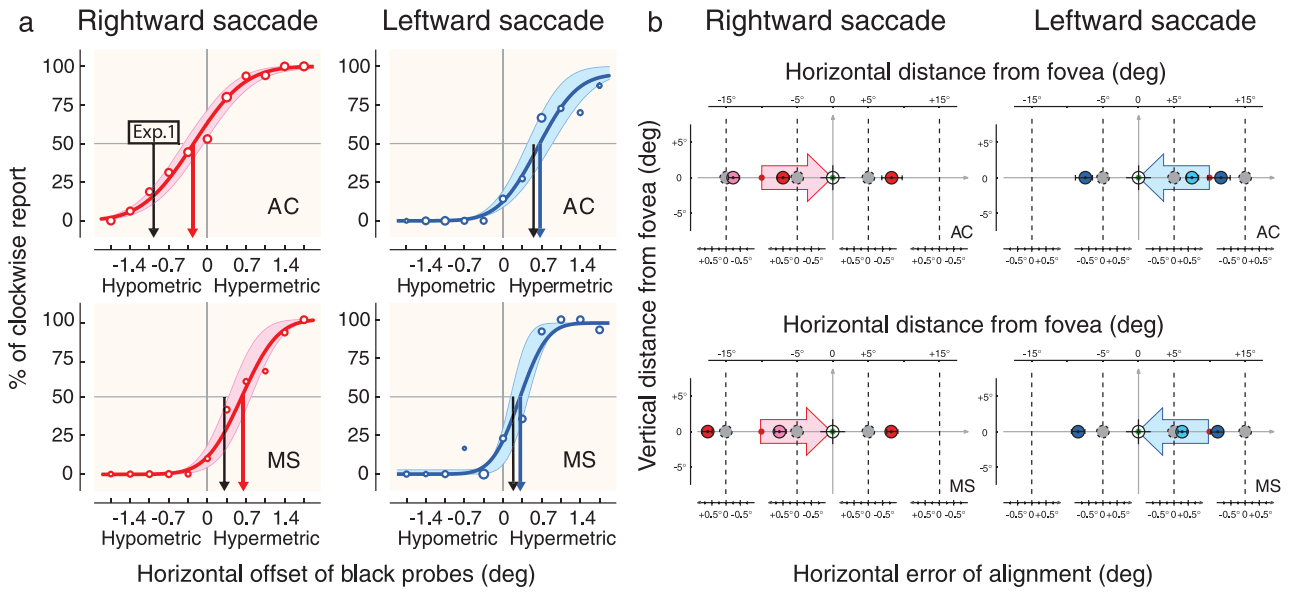


Figure 8. Results of Experiment 2. (a) Percentage of "clockwise" report of two representative locations tested with rightward (red curves) and leftward (blue curves) "correct saccade" trials for both participants. Psychometric functions were fitted to estimate the point of subjective verticality (PSV), i.e., the amount of horizontal offset of probes leading to equal response of clockwise and counterclockwise deviations from vertical (see red and blue arrows). Shaded areas represent 95% confidence interval computed by bootstrapping. Black arrows represent correction biases observed in Experiment 1 for the same participant at the same location and saccade direction. (b) Maps of horizontal errors of alignment. Each row corresponds to rightward and leftward saccade trials for both participants. Conventions used here are described in Figure 4. The locations of the 4 representative cases displayed in (a) are shown here with light red dots for rightward saccade and with light blue dots for leftward saccade trials.

close to the moment at which the green fixation dot changed its position on the screen, i.e., during the 200 ms that separated the probe presentations (Figure 7). To be sure that apparent motion was tested trans-saccadically, we sorted trials in 3 categories: "early saccade," "late saccade," and "correct saccade." On "early saccade" trials, saccades landed before the disappearance of the first probe (see light green lines in Figure 7), whereas on "late saccade" trials, saccades start after the appearance of the second probe. In both cases, the participant might be able to see both probes on one fixation, so the motion would not be strictly trans-saccadic. On the other hand, "correct saccade" trials (see dark green lines in Figure 7) were appropriate for tests of trans-saccadic motion. The horizontal eye positions as a function of the type of saccade trials are displayed in Figure 7. For the first participant, AC, correct saccade trials represent 74.0% of all trials (880/1190), early saccade trials 25.7% (306/1190), and late saccade trials 0.3% (4/1190). For the second participant, MS, the proportions were, respectively, 60.3% (917/1521), 39.4% (600/1521), and 0.3% (4/1521).

In this experiment, the two probes were horizontally displaced from each other to a variable degree and participants were instructed to report the tilt direction of apparent motion perceived while they followed a green dot moving back and forth between the two fixation locations. We quantified the horizontal deviation from accurate saccade correction by determining the horizontal offset between the two probes required to obtain a level of 50% clockwise or counterclockwise reports of motion. This level is determined as the point of subjective verticality (PSV) where the horizontal displacement between probes led to the perception of a trans-saccadic vertical apparent motion. We measure PSV values for all trials as well as for only "correct saccade" trials.

Two representative psychometric curves for "correct saccade" trials are displayed in Figure 8a for each participant and drawn again on maps of horizontal error of alignment in Figure 8b. As in Experiment 1, these results give us the opportunity to observe the direction and the amount of correction for the saccade. Thus, for probes presented 10° to the left or to the right of screen center (Figure 8b), the corrections were always hypometric (undercompensated) for AC and almost always hypometric for MS (3 out 4 cases). As in Experiment 1, the corrections for probes presented between fixation and saccade target (5° left or right of screen center) were hypermetric (overcompensated) for both participants. The average absolute biases (where 0° bias represents accurate, spatiotopic correction) across all locations and saccade directions for both participants were 0.66° ± 0.04° (AC: 0.61° ± 0.27°; MS: 0.70° ± 0.32°). These biases in saccade

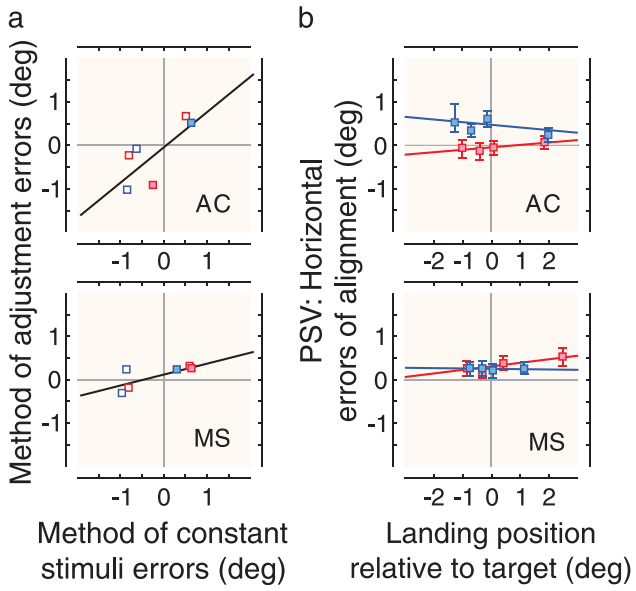


Figure 9. Correlations. (a) Correlation of the observed biases obtained with the method of adjustment in Experiment 1 and those from method of constant stimuli of Experiment 2 for the "correct saccade" trials only. The 6 points represent the combination of the 2 directions of saccade and the 3 spatial locations tested. Filled dots correspond to the two representative conditions displayed in Figure 8a. (b) Correlation between saccade landing position relative saccade target and PSV values observed for rightward (red square) and leftward (blue square) representative saccade trials for each participant. PSV values are plotted against the average landing position relative saccade target for four bins of equal sample size. Error bars indicate 95% confidence interval.

correction showed a significant variation across locations ($F(5, 5) = 9.71$, $p < 0.05$).

How similar are the results in this experiment compared to those of the first experiment? How valid were the tests of spatiotopic apparent motion based on the subjective saccade synchronization in Experiment 1? First, there is a significant correlation between the adjustment settings of the first experiment (for these same three locations) and the PSV values of the second experiment for both participants. This is true when using PSV values based on all trials (AC: $R^2 = 0.85$, one-tailed t-test, $p < 0.05$; MS: $R^2 = 0.80$, one-tailed t-test, $p < 0.05$) as well as only "correct saccade" trials (Figure 9a; AC: $R^2 = 0.76$, one-tailed t-test, $p < 0.05$; MS: $R^2 = 0.74$, one-tailed t-test, $p < 0.05$). The magnitude of the deviation from accurate correction increased in the second experiment to 0.66° ± 0.04° (average for both participants) versus 0.38° ± 0.09° in the first experiment (for these same three locations along the horizontal meridian), but this change was not significant for either participant. We also observed here a small tendency of compression toward fixation target as described in Experiment 1, for both directions of saccade for one participant (AC) but only one direction of saccade for the other (leftward saccade, MS). These results suggest that the distribution of correction errors obtained in the first experiment (Figures 4 and 5) reflected the underlying processes of correction for saccades and were not due to the method of measurement nor to inaccuracies of saccade execution.

Next, we used the data from the early and late saccade trials from this second experiment to examine how imprecise saccade timing would affect the results in the first experiment where eye movements were not monitored. There was a fair proportion of early saccades in the second experiment (25 to 40%), and if early saccades had similar frequency in the first experiment, they would not have been discarded and may have affected the results. Because early and late saccade trials for both participants were not equally distributed across all combinations of variables, we did not fit psychometric curves to determine the PSV values of "incorrect" saccade trials. Instead, we subtracted PSV values obtained with all saccade trials from those obtained with only correct saccade trials to determine the magnitude of the effect of all the "incorrect" saccade trials (i.e., "all saccade trials" = "incorrect saccade trials" + "correct saccade trials"). Using this subtraction method, we observe that "incorrect" saccade trials lead to significantly smaller biases (0.12° ± 0.02°, $t(2) = 20.91$, $p < 0.001$) than "correct" saccade trials (0.66° ± 0.04°) and almost no bias when motion probes were presented at the central location between fixation and saccade target (0.02° ± 0.001°). Thus, on trials where a direction judgment could be made without a saccade intervening between the first and second stimuli, there was, unsurprisingly, little or no misjudgment of the vertical displacement. In this case, the only effect of a mixture of inappropriately early or late saccades in Experiment 1 would be to reduce the correction biases we measured. The smaller effect with inappropriate timing is one possible source for the larger deviations measured here in the "correct saccade" trials than were measured in Experiment 1.

Finally, we analyzed whether the saccade landing location affected the direction judgments. In particular, the deviations from vertical motion that we measured may not be due to errors of saccade correction but errors of saccade landing. In other words, the compensation for saccades might be accurate, but errors in the saccade landing may introduce an error in the expected post-saccadic location of the initial probe stimulus relative to its pre-saccadic location on the monitor. A similar question has been studied recently (Collins, Rolfs, Deubel, & Cavanagh, 2009; Ostendorf, Liebermann, & Ploner, 2010) concerning the perceived motion or displacement of a subsequent test relative to the saccade target itself. These authors reported that the judgments of probe position were independent of saccade landing location. To test this question in our display, we analyzed the PSV values as a function of the deviation of the saccade landing site from the saccade target, dividing our data into

four quartiles of deviation. If the deviation of the saccade landing site from the fixation target was source of the misjudgment of the motion direction, the PSV values in each landing site quartile should shift by the same amount as the landing site. Instead, we find relative independence. Figure 9b presents the 4 PSV values obtained by fitting data separated into quartiles of saccade landings for 2 representative spatial locations tested. The figure shows relatively flat functions, indicating that the perceived deviations from vertical did not depend on the landing sites of the saccades. We did not observe any significant correlation for any of the 6 combinations of saccade directions and spatial locations (AC: $0.72 > R^2 > 0.14$, two-tailed t-test, $0.63 > p > 0.15$; MS: $0.80 > R^2 > 0.07$, two-tailed t-test, $0.73 > p > 0.06$). Moreover, if trial-to-trial oculomotor errors caused the deviations of apparent motion from vertical, saccades should, in general, show more undershoot in the case of hypometric results and overshoot in the case of hypermetric results. However, the saccade amplitudes observed for locations with hypometric and hypermetric results have Gaussian distributions with quite similar median values (AC: saccade amplitude medians of 10.51° and 10.62° for locations with hyper- vs. hypometric corrections for vertical motion, respectively; MS: 10.75° and 10.78°, respectively). Kruskal–Wallis non-parametric comparisons of these distributions show no significant differences (AC: $p > 0.72$; MS: $p > 0.91$). Overall, we see no evidence that the deviations from vertical motion are a result of saccade landing errors.

Discussion

In this second experiment, we observed deviations from accurate compensation of the saccade of about 6% of the 10° saccade amplitude for the trials where the motion was strictly trans-saccadic. These errors are similar in magnitude to those observed in Experiment 1 despite the differences in methods. The eye movement recordings in this second experiment showed that participants made early saccades in about a third of the trials, and on those trials, they could have registered both probe locations following the saccade. However, there appears to be little or no misjudgment of vertical motion on those early saccade trials so that the inevitable inclusion of some inaccurately timed saccades in Experiment 1 would have, if anything, reduced the strength of the deviations from spatiotopy but could not create those deviations. Altogether these results confirm that trans-saccadic apparent motion is seen in a roughly spatiotopic rather than in a retinotopic reference frame and that the compensation for eye movements is fairly accurate with errors in the range of 5% to 6% of the saccade length with, in addition, a significant variation in error as a function of location.

Finally, the analysis of saccade landing sites revealed that trial-to-trial oculomotor inaccuracy did not contribute to the deviations in perception of vertical apparent motion. As other studies suggest (Collins et al., 2009; Ostendorf et al., 2010), oculomotor errors are taken into account when the corrections for a saccade are generated so that the visual system can accurately predict where the target should be relative to the landing site.

No-saccade control experiments

Introduction

The analysis used in the two previous experiments assumed that all errors in judging vertical orientation of the motion were due to errors in accurately correcting for the saccades. However, judgments of vertical motion and of the position of the individual probes may be biased at different locations even in the absence of saccades. In these two control experiments, we measure the magnitude of these judgment errors when no saccades are made. Our first control was matched in procedure (9 locations, method of adjustment) and participants to Experiment 1 while our second control was matched in procedure (3 locations, method of constant stimuli) and participants to Experiment 2. The results reveal non-saccade-related biases that, in total, account for about 25% of the errors measured in the first experiments, indicating that compensation for the saccades is somewhat more accurate than those measurements suggested.

We first measure any biases in judging vertical orientation of motion at different locations to determine if any of the deviations measured in the first experiment can be attributed to errors in verticality judgments of the motion in the absence of saccades. Studies investigating verticality perception for lines (without motion) at different eccentricities suggest that participants are quite accurate (for a review, see Mittelstaedt, 1983), at least when their heads are positioned vertically. We now extend these tests to the verticality of apparent motion using exactly the same display as in the first experiment but this time holding fixation throughout (Figure 10a).

We then measure position biases, specifically, the tendency to estimate the location of stimuli as being closer to the fovea than they really are. In our trans-saccadic motion experiments, the first and second stimuli are at different locations relative to the fovea (for example, the first to the right of fixation and the second to the left) so that the foveal biases (Mateeff & Gourevich, 1983) of those two locations may combine to contribute to an apparent deviation from vertical.

Methods

Participants

The four participants of Experiment 1 took part in the verticality motion control experiment (2 authors and 2 participants, age 24–61 years). The two participants of

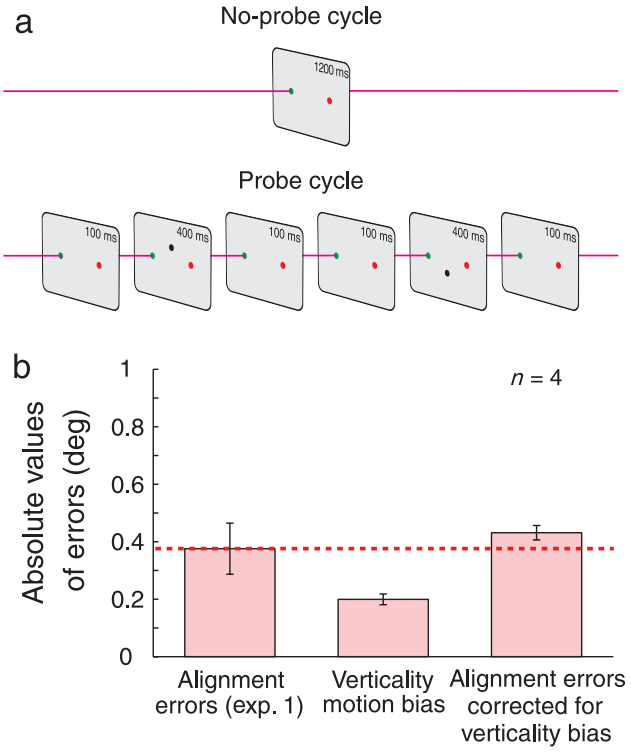


Figure 10. Verticality motion control experiment. (a) Spatial layout of the stimuli for a sample right fixation trial. Participants were instructed to keep fixation on the green dot throughout the trial, composed of alternating "no probe cycles" and "probe cycles." After each "probe cycle," they moved a mouse to adjust the horizontal locations of both probes in subsequent cycles, continuing until they perceived motion as vertical. The magenta line represents the supposed line of gaze during the trial. Probe position and duration were identical to those of Experiment 1. (b) Absolute values of errors for the 4 participants in the saccade task of Experiment 1, in the verticality of motion judgments during fixation, and for the alignment errors with saccades after correction for verticality or motion bias. Error bars indicate *SEM*.

Experiment 2 took part in position control experiment (1 author and 1 participant, age 24–25 years).

Instruments and stimuli

The stimuli, experimental room, display, toolboxes, and computer configurations were identical to those of the first two experiments. Fixation of the right eye was monitored with the same eye-tracking system as in Experiment 2.

Procedure

All participants took part in the verticality control experiment after the first experiment. The two participants who took part in position control experiment completed this last experiment following all the others. For both verticality motion and position controls, each trial began with two circles—one green and one red—displayed on a gray background. Contrary to the saccade tasks of the first two experiments, participants were now instructed to always fixate the green circle that could equiprobably be located 5° to the left or to the right of screen center and remained there throughout the trial.

In the verticality motion control experiment, once fixation was held for at least 200 ms, two circular black probes were presented equiprobably at one of the nine different locations tested during Experiment 1 (Figure 2b). All stimuli sizes and durations of display were identical to those used in both previous experiments. The only major difference was that the green and red circles never exchanged positions. Each "probe cycle" alternated with a "no probe cycle" (Figure 10a) of the same duration (1.2 s), during which no probe was presented. As in Experiment 1, probes were randomly initially presented vertically aligned or with a physical tilt (Figure 2c). Because no significant difference was found between bottom-first (upward motion) and top-first (downward motion) order of presentations of the probes in Experiment 1, they were here always displayed top-first (downward motion). As participants fixate the green circle, they were instructed to use the computer mouse to adjust the horizontal positions of the probes after each downward motion until they perceived the motion to be vertical. Fixation was monitored online and trials were interrupted and randomly replayed later if the eyes crossed a circular boundary with a radius of 2° centered on the green circle or if a blink was detected. All participants ran 8 blocks of 18 trials each (144 trials). Each session was composed of 2 or 3 blocks and always lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min. When we compare this fixation task with the saccade task (Experiment 1) in the Result section below, we correct alignment errors observed during the saccade task for verticality bias measured here. To make the correction, we assume that the direction of the motion can only be perceived in the saccade task following the saccade when information from both locations is available. Following a leftward saccade, then, the apparent motion is seen as occurring to the right of fixation, and vice versa. We therefore subtracted the verticality bias obtained when participants judged motion on the right of fixation from the trans-saccadic measures for leftward saccade trials and vice versa.

In the position control experiment, once fixation was detected for at least 200 ms, a circular black probe was presented one time during 400 ms (Figure 11a). We tested 3 different horizontal locations equally spaced by 10° from center of the screen (same locations tested in Experiment 2). From these three locations on the horizontal midline of the screen, the probe was horizontally displaced with one of 11 equiprobable horizontal offsets from −1.75° (to the left) to +1.75° (to the right) following a constant stimuli procedure. Finally, this probe appeared equiprobably at a top or at a bottom vertical

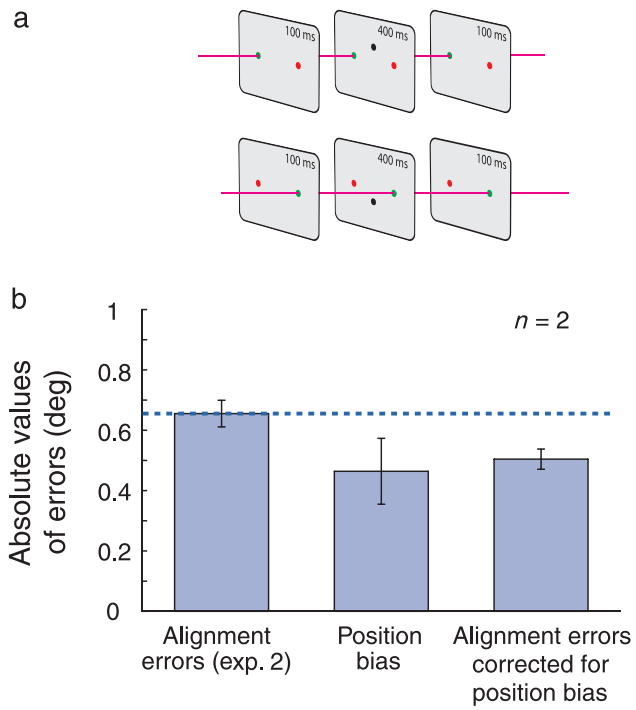


Figure 11. Position control experiment. (a) Spatial layout of the stimuli for a sample rightward saccade simulated trial. In two successive randomly presented trials, participants keep fixation on the green dot located at the right or left of the screen center. The magenta line represents the supposed line of gaze during trials. Participants evaluate the probe position displayed above and then below the horizontal midline with a physical horizontal offset following a method of constant stimuli. (b) Absolute values of errors for the 2 participants in the saccade task of Experiment 2, in the position judgment during fixation, and for the alignment errors with saccade after correction of position bias. Error bars indicate *SEM*.

position, respectively, 1.5° above or below the horizontal center of the screen to test the two motion locations used in Experiments 1 and 2. After each trial, participants report whether the probe was displayed to the left or to the right of a position corresponding to half of the distance between the red and the green dot from the fixation point. One participant ran 8 blocks of 132 trials each (1056 trials) and the other ran 10 blocks (1320 trials). For the analysis of the data, we selected only trials in which fixation was maintained in a 2° radius circle boundary centered on a green dot and trials without blink during all the duration of the trial. This selection left 95.93% of all trials for the first participant (AC: 1013/1056 trials kept) and 99.47% of all trials for the second participant (MS: 1313/1320 trials kept). Each session was composed of 2 to 4 blocks and always lasted less than 15 min. During each session, the eye-tracking system was recalibrated every 8 min. In the Results section below, we correct the absolute magnitude of alignment errors observed in the saccade tasks of Experiments 1 and 2, respectively, with the absolute magnitude of the bias observed in the no-saccade control task for verticality of motion bias and for position bias. We never correct the saccade task results with all the no-saccade task results taken together, because the procedures followed in each of these experiments were different. For Experiment 1 and the control for verticality of motion bias, we used a method of adjustment, while for Experiment 2 and the control for position bias, we used a method of constant stimuli with an eye-tracking correction.

Results and discussion

For the verticality of motion control experiment, we found significant variation in the adjustments for verticality across the retinal locations tested ($F(17, 51) = 2.14$, $p < 0.05$). The absolute size of the deviations was about half that measured with saccades in the first experiment (fixation task: 0.20° ± 0.02°; saccade task: 0.38° ± 0.09°, ns, $t(6) = 1.94$, $p = 0.65$). The verticality motion biases were, however, mostly independent of or slightly in the direction opposite to the alignment deviations measured with saccades ($0.08 > R^2 > 0.002$, two-tailed t-test, $0.86 > p > 0.26$), so that when we corrected the measures obtained for each participant in the first experiment with those obtained in this fixation task (Figure 10b), the absolute magnitude of correction errors was unaffected (before correction: 0.38° ± 0.09; after correction: 0.43° ± 0.02°) and we still found a significant variation across the retinal locations tested ($F(17, 51) = 6.36$, $p < 0.001$). These biases in judging verticality of apparent motion, therefore, do not explain the errors of correction for saccades observed in the first experiment.

Our second control task, for position, measured the effect of position biases (Mateeff & Gourevich, 1983) at the different locations corresponding to those presented in the apparent motion tests. For example, if the first stimulus in the apparent motion sequence is perceived closer to the fovea than it was, and following the saccade, the second stimulus is also perceived closer to the new position of the fovea, then the perceived motion direction will deviate from vertical.

To simulate the effect of position biases on the trans-saccadic motion stimuli, we used separate trials with eyes fixed for the pre-saccadic (e.g., to the left of fixation) and post-saccadic locations (e.g., to the right) to measure the bias at all appropriate locations (Figure 11a). From these data, we computed the combined bias for the conditions tested in Experiment 2. First, we observed small but significant correlations between the results obtained in the saccade trials and the simulated intersaccadic position biases for both our participants (AC: $R^2 = 0.51$, one-tailed t-test, $p < 0.01$; MS: $R^2 = 0.36$, one-tailed t-test, $p < 0.05$).

Second, we evaluate the magnitude of errors corrected for position bias (Figure 11b) and found a decrease from 0.66° ± 0.04° of alignment errors in the saccade task to 0.50° ± 0.03° of alignment errors corrected for position bias. These results suggest that the position bias explained about 23% of the amplitude of the alignment errors observed in Experiment 2 and about 40 to 50% of the variance observed. The horizontal errors of alignment (Experiment 2) now corrected for position bias still show significant variation ($F(5, 5) = 5.02$, $p < 0.05$) across the 6 different locations (3 locations, two directions of saccade), although this ANOVA with only 2 participants can only be considered as suggestive.

To summarize the results in these two control tasks without eye movements, we found systematic biases in judgments of verticality of motion between two successive stimuli and in judgments of the perceived location of single dots. We estimated the proportion of the saccade correction errors explained by these biases and found that the vertical motion bias had little effect whereas position biases were correlated with the deviations reported in Experiment 2 (R^2 of 0.51 and 0.36 for the two participants). When corrected for position bias, correction errors still represented about 5% of saccade length and showed variation across locations.

General discussion

Normally, we see objects moving only when they actually move in the world and not whenever our eyes move. Our visual system corrects for eye movements. However, what happens if something moves at the same time as our eyes move? Change blindness (Grimes, 1996; Henderson & Hollingworth, 1999) demonstrates that we are unable to see displacements that occur at the time of a saccade, unless it is the displacement of an attended item (O'Regan et al., 1999). Even then, if an attended target is displaced along the direction of the saccade and the target is present when the saccade lands, significant shifts may be undetected (Bridgeman et al., 1975). Nevertheless, under some conditions, shifts at the time of the saccade are seen: for large displacements (Bridgeman et al., 1975), or displacements orthogonal to the saccade (Niemeier et al., 2003), or displacements where the target reappears after the saccade has landed (Deubel et al., 1996). Our stimuli had all three of these properties, maximizing the visibility of the trans-saccadic motion. The question we addressed was whether the perceived motion would be veridical, that is, appropriate to the displacement in spatial coordinates as opposed to retinal coordinates. Our two first experiments demonstrated that a vertical motion straddling a horizontal saccade was seen roughly in spatial coordinates. This result extends the Rock and Ebenholtz (1962) report of simple spatiotopic apparent motion to a condition where the stimulus motion was orthogonal to the saccade and at non-foveal locations. This allowed us to measure the accuracy of the correction for the saccade at different positions in the visual field.

We determined the accuracy of the correction at several locations (9 in the first experiment, 3 in the second) within about 15 deg around the fovea for both leftward and rightward saccades. The deviations between the perceived motion and the actual motion as it occurs in space suggest that biases in the correction represent about 5% of the saccade length and that they vary significantly across locations. We observed variations in these local biases across participants and these idiosyncratic patterns were stable over test–retest intervals of up to 3 months. The second experiment showed that these errors held up when measured using a different method (constant stimuli instead of adjustment) and after sorting trials to limit the analysis to trials where the saccade occurred between the presentation of the two positions of the apparent motion stimulus. Two control experiments evaluated the contribution of biases of verticality of motion direction and position seen in the absence of eye movement. The local biases in judging verticality had little or no effect whereas the position biases could account for about a quarter of the amplitude of the local biases in saccade correction.

What does this mean for the mechanisms of saccade correction?

Following Rock and Ebenholtz (1962) and Fracasso et al. (2010), our results show that we can see a motion in the world that is coincident with an eye movement and that we do not see it in retinal coordinates but in roughly spatial coordinates. Of most interest was the local variation in the correction for the saccades, a result that argues against global approaches to space constancy and for local corrections. It is very unlikely that the probes themselves, presented at different locations, were the source of the position-dependent variation in corrections for the saccades. In our stimulus, the saccade target itself never moved and was present when the saccade landed. The second motion probe appeared about 100 ms after the saccade so it is difficult to argue that the probe location affected the correction for the saccades. Even if it did, the effect should have been larger for probes nearer the fovea (Irwin et al., 1994), but we did not see this pattern as some of the largest errors of correction were for the more distant probes (Figures 4 and 5).

We suggest therefore that our results support local correction mechanisms like the remapping process seen in single cell activity on saccade control centers (Gottlieb et al., 1998; Kusunoki et al., 2000; Wurtz, 2008). The correction in this remapping case is applied to individual attended targets (Rolfs et al., 2011), and even though the same efference copy vector drives the correction for each

target, the conversion of the vector to a shift on the roughly log polar coordinates of the saccade control maps is idiosyncratic to each location and direction (Cavanagh et al., 2010). The two models of this process (Keith & Crawford, 2008; Quaia et al., 1998) require that the link between the target location and the saccade vector that predicts the post-saccadic location must be learned independently for each location and saccade.

As explained above, our non-uniform results for the different spatial locations tested challenge any alternative explanations sustaining a global or uniform process of saccade correction for the entire visual field. This includes also explanations in terms of incomplete saccadic suppression or a lingering attentional trace at the retinotopic location (Golomb, Chun, & Mazer, 2008; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010). These contributions from retinotopic factors would be seen as hypometric errors (undercompensations) that should be similar for all locations. In contrast, we observed many hypermetric errors (for example, for the central test location as in Movies 1, 2, and 3) and significant local variation.

The results argue against a simplistic global correction mechanism where the compensation for the eye movement is the same at all locations. Nevertheless, any detailed implementation of a global correction, even models that do not call on extra-retinal information (Bridgeman, 2007; O'Regan et al., 1999), will have to deal with the application of the global correction to local targets that are not the saccade target. This may introduce local variations of correction as well, so our results act more to constrain global models of compensation than to rule them out completely.

An additional property of correction for saccades was reported by Fracasso et al. (2010) who showed that the apparent motion across a saccade not only keeps track of the pre-saccadic location but also the pre-saccadic shape. Specifically, for a target that changed shape between its pre- and post-saccadic presentations, the shape change was seen as a transformational motion (Tse, Cavanagh, & Nakayama, 1998) rather than a shape replacement. This result suggests that correction for saccades not only updates location but also keeps track of target shape. There is recent evidence of this in an fMRI study of remapping (Knapen, Swisher, Wolfe, Tong, & Cavanagh, 2010) that showed a trans-saccadic transfer of a shaped region of BOLD activation that was isomorphic to the target shape.

What about mislocalization and compression?

Our results are far from the first to show an effect of location on the perceived position errors of brief probes. Several key papers have established that peri-saccadic mislocalization and compression effects (Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Matin & Pearce, 1965; Morrone et al., 1997) can be as large as the saccade itself and that their amplitude depends on the test position. We will outline first how our tests differ from those of the mislocalization and compression experiments and we then consider what would happen if, indeed, some of these compression effects contributed to the correction errors we report. First the differences: our 400-ms stimuli are not very brief compared to the typical 25 ms or less in the peri-saccadic mislocalization and compression tasks. In addition, the timing is very different. Our first probe is removed about 100 ms before and the second probe presented about 100 ms after the saccade whereas peri-saccadic mislocalization is minimal at these intervals. For these reasons, we suggest that our results reflect the end product of the correction for eye movements and not the rapidly changing intermediate states that may be revealed by brief presentations within 50–75 ms of the saccade.

Nevertheless, given that our effect is so much smaller (5% rather than 100% of saccade amplitude) perhaps our smaller effect is just the size the compression effects would have at these long durations. Here the evidence is completely the opposite. For example, for probes presented midway between the fixation and the saccade target (see Movies 2 and 3), our results suggest that the first probe is seen, after the saccade has landed, as having been further from the saccade target, not closer as the compression effect would predict. In addition, the compression studies would predict compression toward the saccade target (Morrone et al., 1997; Ross et al., 1997); however, if anything, we found a small tendency to compression toward the fixation target. So we conclude that our local variations in saccade correction are stable, final products of the correction process and unrelated to the peri-saccadic mislocalization effects.

Why do we not see these deviations from space constancy every time we move our eyes?

Finally, given that we find an inaccuracy of about 5% in the correction for saccades, we must ask why do we not notice these errors in everyday life. First, the most noticeable errors may be those for the saccade target itself, which lands on or near the fovea at the end of the saccade. In our experiments, we never measured locations closer than 5° to the fovea, but a recent article by Collins et al. (2009) did. They also report a bias of about 5% for displacements of the saccade target itself. Specifically, if the saccade target was removed during the eye movement and replaced at its original location with a delay of 200 ms, it appeared to have moved forward—in the direction of the saccade, a hypermetric correction. So why are even

these fovea displacements not seen? Deubel et al. (2010) have shown that we are very insensitive to trans-saccadic target displacements if the target is present when the saccade lands, as it is of course for our everyday saccades around real scenes. These authors also showed that we are much more sensitive to the same displacements if there is a blank temporal gap of 50 ms or more between the saccade landing (with no target present) and the representation of the target. In our stimuli, and in those of Collins et al. (2009), there was a post-saccadic delay before the presentation of the new location of the target so this should accentuate its visibility. However, we do suggest that these inaccuracies of spatial constancy may be noticed for attended targets even without blanking, although of course they go unnoticed for unattended parts of the visual field (Cavanaugh & Wurtz, 2004; O'Regan et al., 1999). For example, with a saccade from the left edge of this page to the right edge, a small but consistent displacement of the text in the direction opposite to the saccade might be visible. The displacement is, at best, subtle and easily ignored. In our experiments (see Movie 1), we make this subtle displacement clearly visible by removing the stimulus during the saccade and replacing it only later, about 100 ms after the saccade.

Conclusion

Using an apparent motion test, we demonstrate that trans-saccadic displacement is perceived in roughly spatial rather than retinal coordinates. This spatiotopic apparent motion provides a simple method for measuring the accuracy of the processes that correct for eye movements and shows that there is a significant local variation in the corrections. These local variations suggest that space constancy depends on local corrections consistent with the physiological remapping of individual attended targets.

Acknowledgments

We are grateful to J. K. O'Regan for his comments on our work, to members of the Centre Attention and Vision (AV, CB, FVV, MR, RA, TBD, and TK), and to E. Parison. This research was supported by a *Chaire d'Excellence* Grant to PC and a French *Ministère de l'Enseignement Supérieur et de la Recherche* Grant to MS.

Commercial relationships: none.
Corresponding author: Martin Szinte.
Email: martin.szinte@gmail.com.
Address: Laboratoire Psychologie de la Perception, Center Attention & Vision, Université Paris Descartes – CNRS, 45, rue des Saints-Pères, Paris 75006, France.

References

Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychological Research, 32,* 185–218.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Breitmeyer, B. G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. *Acta Psychologica, 52,* 175–196.

Bridgeman, B. (2007). Efference copy and its limitations. *Computers in Biology and Medicine, 37,* 924–929.

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research, 15,* 719–722.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences, 17,* 247–258.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences, 14,* 147–153.

Cavanaugh, J., & Wurtz, R. H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience, 24,* 11236–11243.

Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision, 9*(5):29, 1–9, http://www.journalofvision.org/content/9/5/29, doi:10.1167/9.5.29. [PubMed] [Article]

Cornelissen, F. W., Peter, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers, 34,* 613–617.

Currie, C. B., McConkie, G. W., Carlson-Radvansky, L. A., & Irwin, D. E. (2000). The role of the saccade target object in the perception of a visually stable world. *Perception & Psychophysics, 62,* 673–683.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research, 38,* 3147–3159.

Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Research, 50,* 249–259.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research, 36,* 985–996.

Duhamel, Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in

parietal cortex by intended eye movements. *Science, 255,* 90–92.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, 103,* 7192–7197.

Fracasso, A., Caramazza, A., & Melcher, D. (2010). Continuous perception of motion and shape across saccadic eye movements. *Journal of Vision, 10*(13):14, 1–17, http://www.journalofvision.org/content/10/13/14, doi:10.1167/10.13.14. [PubMed] [Article]

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields: III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology, 64,* 489–508.

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The native coordinate system of spatial attention is retinotopic. *Journal of Neuroscience, 28,* 10654–10662.

Golomb, J. D., Pulido, V. Z., Albrecht, A. R., Chun, M. M., & Mazer, J. A. (2010). Robustness of the retinotopic attentional trace after eye movements. *Journal of Vision, 10*(3):19, 1–12, http://www.journalofvision.org/content/10/3/19, doi:10.1167/10.3.19. [PubMed] [Article]

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature, 391,* 481–484.

Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In K. Akins (Ed.), *Perception Vancouver studies in cognitive science* (pp. 89–110). England: Oxford University Press.

Henderson, J. M., & Hollingworth, A. (1999). The role of fixation position in detecting scene changes across saccades. *Psychological Science (Wiley-Blackwell), 10,* 438.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics, 45,* 162–174.

Irwin, D. E., McConkie, G. W., Carlson-Radvansky, L. A., & Currie, C. (1994). A localist evaluation solution for visual stability across saccades. *Behavioral and Brain Sciences, 17,* 265–266.

Keith, G., & Crawford, J. (2008). Saccade-related remapping of target representations between topographic maps: A neural network study. *Journal of Computational Neuroscience, 24,* 157–178.

Knapen, T., Swisher, J., Wolfe, B., Tong, F., & Cavanagh, P. (2010). Phase-encoded fMRI investigation of retinotopic remapping responses [Abstract]. *Journal of Vision, 10*(7):510, 510a, http://www.journalofvision.org/content/10/7/510, doi:10.1167/10.7.510.

Koch, C., & Deubel, H. (2007). How postsaccadic visual structure affects the detection of intrasaccadic target displacements. In R. P. G. van Gompel, M. H. Fisher, W. S. Murray, & R. L. Hill (Eds.), *Eye movements: A window on mind and brain* (pp. 193–212). Oxford, UK: Elsevier.

Kusunoki, M., Gottlieb, J. P., & Goldberg, M. E. (2000). The lateral intraparietal area as a salience map: The representation of abrupt onset, stimulus motion, and task relevance. *Vision Research, 40,* 1459–1468.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403,* 892–895.

Mateeff, S., & Gourevich, A. (1983). Peripheral vision and perceived visual direction. *Biological Cybernetics, 49,* 111–118.

Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin, 81,* 899–917.

Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science, 148,* 1485–1488.

McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance, 22,* 563–581.

Mittelstaedt, H. (1983). A new solution to the problem of the subjective vertical. *Naturwissenschaften, 70,* 272–281.

Morrone, M. C., Ross, J., & Burr, D. C. (1997). Apparent position of visual targets during real and simulated saccadic eye movements. *Journal of Neuroscience, 17,* 7941–7953.

Niemeier, M., Crawford, J. D., & Tweed, D. B. (2003). Optimal transsaccadic integration explains distorted spatial perception. *Nature, 422,* 76–80.

O'Regan, J. K., Rensink, R. A., & Clark, J. J. (1999). Change blindness as a result of 'mudsplashes'. *Nature, 398,* 34.

Ostendorf, F., Liebermann, D., & Ploner, C. J. (2010). Human thalamus contributes to perceptual stability across eye movements. *Proceedings of the National Academy of Sciences, 107,* 1229–1234.

Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442.

Quaia, C., Optican, L. M., & Goldberg. (1998). The maintenance of spatial accuracy by the perisaccadic remapping of visual receptive fields. *Neural Networks, 11,* 1229–1240.

Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To see or not to see: The need of attention to perceive changes in scenes. *Psychological Science, 8,* 368–373.

Rock, I., & Ebenholtz, S. (1962). Stroboscopic movement based on change of phenomenal rather than retinal location. *The American Journal of Psychology, 75,* 193–207.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience, 14,* 252–256.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccade. *Nature, 386,* 598–601.

Sommer, M. A., & Wurtz, R. H. (2004). What the brain stem tells the frontal cortex: II. Role of the SC–MD–FEF pathway in corollary discharge. *Journal of Neurophysiology, 91,* 1403–1423.

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature, 444,* 374–377.

Sperry, R. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology, 43,* 482–489.

Tse, P., Cavanagh, P., & Nakayama, K. (1998). The role of parsing in high-level motion processing. In T. Watanabe (Ed.), *High level motion processing* (pp. 249–266). Cambridge, MA: MIT Press.

Umeno, M. M., & Goldberg, M. E. (2001). Spatial processing in the monkey frontal eye field: II. Memory responses. *Journal of Neurophysiology, 86,* 2344–2352.

Volkmann, F. C. (1986). Human visual suppression. *Vision Research, 26,* 1401–1416.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften, 37,* 464–476.

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63,* 1293–1313.

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics, 63,* 1314–1329.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research, 48,* 2070–2089.

4.2 Can we visualize remapping as it occurs?

4.2.1. Objectives and summary of results

The results of our first study and the physiological literature suggest that “remapping” plays a critical role in recovering object position across saccades. This process is not instantaneous, however. In physiological reports, some cells start showing remapped responses before the saccade (Duhamel et al., 1992), but the majority start at the time of the saccade and even after the onset of the saccade (Kusunoki & Goldberg, 2003; Nakamura & Colby, 2002). There are many behavioral experiments that present brief probes around the time of a saccade and ask observers to report, after the saccade, where the probe had been presented. These studies find large mislocalization effects (see the introduction to the thesis) and it has been proposed (Burr & Morrone, 2011; Ross et al., 2001) that these reflect the intermediate stages of remapping, the saccade compensation process.

We therefore wanted, in this second study, to devise a stimulus that would allow us to directly visualize remapping as it occurs rather than test the memory of the location a single probe later. To do so, we used a probe moving on a linear path before, during, and after a saccadic eye movement. With this simple, continuously moving stimulus we can visualize the temporal as well as the spatial dynamics of remapping. Our new method also allowed us to compare our visualization results to the previous findings.

In our experiments, a probe moved from the top to the bottom of the screen at a constant speed for 500 ms and observers executed a leftward or rightward saccade across the probe’s path when it was approximately midway in its descent. Observers reported that the motion trace of the probe appeared to be broken into two straight segments that did not line up, with the post-saccadic portion offset in the saccade direction relative to the pre-saccadic portion. To measure the misalignment between the pre- and post-saccadic segments, we introduced a blank in the central 200 ms bracketing the saccade and required that observers make relative judgments of the post against the pre-saccadic traces. To bring the two segments into alignment, observers had to physically shift the post-saccadic segment, in the direction opposite that of the saccade, by approximately one-fifth of the saccade amplitude (about 3° overcompensation for a 15° saccade). This result indicated that the pre-saccadic motion trace was corrected for the effect of the saccade and perceived in roughly spatiotopic rather than retinotopic coordinates. However, the effect of the saccade was overcompensated, moving the pre-saccadic trace too far.

Subsequently, to measure the timing of the break between the two segments, we presented the entire motion path with a counter-shift, cancelling the over-correction at different times relative to the saccade. We asked observers to report if the motion trajectory appeared to be a continuous linear trace or not. When the moving probe was physically offset at roughly the same time as the saccade-induced shift, observers frequently reported an impression of linear continuity. By evaluating the time profile of the continuity reports we identified the moment at which the pre-saccadic trace was shifted to its appropriate, nearly spatiotopic location. We found that this process occurred at about the

midpoint of the saccade, suggesting that, at a perceptual level, the compensation is in place when the saccade lands. Finally, we compared our results to a study reporting no misalignment between the pre- and post-saccadic trace (Honda, 2006). Even with settings similar to those used in Honda's study, we still found the same misalignment.

Contrary to previous behavioral reports of peri-saccadic mislocalization (see the introduction to the thesis), the pre-saccadic portion of the trace was not seen to jump in the direction of the saccade as it does on the retina, nor did it make a curve toward the saccade target and then back to the spatial path as would be expected from peri-saccadic compression (Ross et al., 1997) or a three-part curve as expected from peri-saccadic mislocalization (Honda, 1989; Matin & Pearce, 1965). Instead, the continuous motion trace was seen as two misaligned but linear segments, with the pre-saccadic segment shifted in the direction opposite to the saccade. Moreover, the difference with our results and these mislocalization effects let us suggest that the pre-existing position information of the motion probe appeared to outweigh any visualization of mislocalized objects, suggesting that "grandfathering" suppresses the large mislocalizations, or that they are only introduced by brief stimuli.

The pattern of perceived positions that actually represents the dynamic, intermediate steps of remapping remains to be determined, but whatever the case for these intermediate values, we find a permanent mismatch between the pre- and the post-saccadic motion traces.

Temporal dynamics of remapping captured by peri-saccadic continuous motion

Martin Szinte
Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité; CNRS UMR 8158, Paris, France

Mark Wexler
Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité; CNRS UMR 8158, Paris, France

Patrick Cavanagh
Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité; CNRS UMR 8158, Paris, France

Different attention and saccade control areas contribute to space constancy by remapping target activity onto their expected post-saccadic locations. To visualize this dynamic remapping, we used a technique developed by Honda (2006) where a probe moved vertically while participants made a saccade across the motion path. Observers do not report any large excursions of the trace at the time of the saccade that would correspond to the classical peri-saccadic mislocalization effect. Instead, they reported that the motion trace appeared to be broken into two separate segments with a shift of approximately one-fifth of the saccade amplitude representing an overcompensation of the expected retinal displacement caused by the saccade. To measure the timing of this break in the trace, we introduced a second, physical shift that was the same size but opposite in direction to the saccade-induced shift. The trace appeared continuous most frequently when the physical shift was introduced at the midpoint of the saccade, suggesting that the compensation is in place when the saccade lands. Moreover, this simple linear shift made the combined traces appear continuous and linear, with no curvature. In contrast, Honda (2006) had reported that the pre- and post-saccadic portion of the trace appeared aligned and that there was often a small, visible excursion of the trace at the time of the saccade. To compare our results more directly, we increased the contrast of our moving probe in a third experiment. Now some observers reported seeing a deviation in the motion path but the misalignment remained present. We conclude that the large deviations at the time of saccade are generally masked for a continuously moving target but that there is nevertheless a residual misalignment between pre- and post-saccadic coordinates of approximately 20% of the saccade amplitude that normally goes unnoticed.

Keywords: saccade, remapping, spatial vision, continuous motion

Citation: Szinte, M., Wexler, M., & Cavanagh, P. (2012). Temporal dynamics of remapping captured by peri-saccadic continuous motion. *Journal of Vision, 12*(7):12, 1–18, http://www.journalofvision.org/content/12/7/12, doi:10.1167/12.7.12.

Introduction

Our visual world remains stable despite continual retinal shifts caused by eye movements. With every saccade, the perceived locations assigned to points on the retina must be updated to maintain their correspondence with the objects in the world. Single cell studies (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990) have shown that just before a saccade, cells in several areas respond to stimuli that are outside their receptive fields but that will fall on them after the saccade. These authors noted that this "remapping," might play a critical role in reassigning perceived locations and maintaining space constancy. Behaviorally, many authors have seen this remapping as the source of the mislocalizations of position reported for brief flashes presented within 100 ms of the saccade (Lappe, Awater, & Krekelberg, 2000; Matin & Pearce, 1965; Ross, Morrone, & Burr, 1997; see review of Schlag & Schlag-Rey, 2002). Nevertheless, one concern about these observations is that measurement relies on a delayed report of the remembered briefly flashed location. Several studies have used flickering probes (Hershberger, 1987; Sogo & Osaka, 2001; Watanabe, Noritake, Maeda, Tachi, & Nishida, 2005) to visualize any mislocalizations as relative displacements between successive flashes as they happen. For sequences of flashes triggered during the saccade, the flickering dot was seen as an array of points whose individual

doi: 10.1167/12.7.12 Received March 3, 2012; published July 24, 2012 ISSN 1534-7362

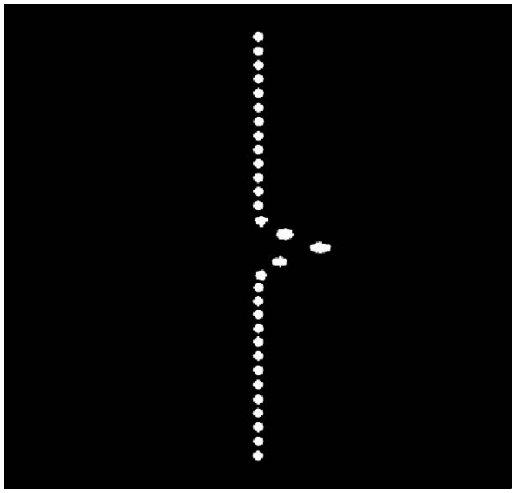


Figure 1. Schematic illustration of typical patterns of distorted trajectories observed in the 302 ms condition of Honda (2006) for a rightward saccade. The stimuli used was composed of 31 adjacent LEDs flashed in sequence, each for 2 ms with an inter-stimulus interval (ISI) of 8 ms. The resulting motion trajectory lasted 302 ms and traversed 18° vertically, lying midway between the fixation and saccade points that were themselves separated by 18°. Two observers reported seeing brief excursions as depicted here in one-third to one-half of the trials. The deviation lasted about 50 ms, going in the direction of the saccade, whereas the pre- and post-saccadic portions of the trace were always aligned (adapted from figure 2c of Honda, 2006).

locations corresponded to the mislocalizations seen for single flashes (Hershberger, 1987). However, if the flickering probe started flickering before the saccade, and specifically at the time of peri-saccadic mislocalization and compression, little or no mislocalization was reported, as if well-established position information overrode or stabilized any shifts that might have been seen for a single flash (Sogo & Osaka, 2001; Watanabe et al., 2005). The pre-existing position information appeared to outweigh any visualization of peri-saccadic mislocalization. Here we report a closely related perceptual measure, a moving probe, first used by Honda (2006), to determine if this probe will reveal peri-saccadic mislocalization as an easily seen, visual pattern.

Honda (2006) used a linear array of LEDs to present a moving probe and asked observers to make a saccade across this motion path. Following the saccade, observers drew the perceived motion trajectory. For very brief motion traces (38 ms and 52 ms) that overlapped with the saccade, the observers drew large curving mislocalizations in the apparent trace. According to Honda, these shifts were consistent with the estimates of mislocalization made from single flashes. However, if the motion probe had a longer duration (302 ms) so that it started before and ended after the saccade, observers reported seeing a straight trace with the pre- and post-saccadic segments aligned, and occasionally with a small deviation away from and then back to the motion path at the time of the saccade (Figure 1). Honda's (2006) moving probe therefore did not appear to offer any further insight into mislocalization than the stationary probes of earlier experiments.

Nevertheless, we were interested in two aspects of the results from Honda's longer duration (302 ms) trace. First, when the excursion was seen (one-third of the trials for the first observer, and fewer than half of the trials for the second observer in Experiment 1), it was quite brief and small, as opposed to the properties that we would expect from the single flash experiments of peri-saccadic mislocalization and compression. In these experiments, brief flashes are mislocalized in a range of 150 ms to 200 ms around the saccade and have amplitude as large as the saccade itself (Lappe et al., 2000; Matin & Pearce, 1965; Ross et al., 1997; see review of Schlag & Schlag-Rey, 2002). Second, whether Honda's observers saw the excursion, they always drew the trace as aligned before and after the saccade. In contrast, our earlier study (Szinte & Cavanagh, 2011) found that the pre- and post-saccadic locations seen for a target in apparent motion across a saccade did not appear aligned. Instead, the results of that study suggested that in correcting for the shift of the saccade, the position of the pre-saccadic dot had been over-compensated by about 5%.

We see two reasons why Honda's results might differ from ours and from the earlier peri-saccadic mislocalization findings. First, Honda's report of an aligned trace before and after the saccade may have been a result of the continuous presence of the motion. The continuous trace provides a location reference for the probe position as the dot moves down the screen. Just as the pre-existing flicker probe suppresses temporary mislocalizations seen just before and after the saccade (Sogo & Osaka, 2001; Watanabe et al., 2005), the moving position reference may also suppress the trans-saccadic shift in coordinates (Szinte & Cavanagh, 2011) that remains uncorrected over larger time scales. Second, to capture the excursions in the motion trace, Honda's observers only made hand-drawn reports of their percept and so may have missed the misalignment and the large excursion away from and back to the vertical motion path at the time of the saccade. In other words, Honda's technique may have allowed a better visualization of mislocalization than the stationary flickering probes, but the deviation may have been too brief and/or dim to be reported in the hand-drawn measures of his participants.

To test the continuous motion stimulus more parametrically, we used a similar stimulus composed of a salient probe moving down the display before,

during and after saccade (Movie 1 and Figure 2a) that was fairly close in timing and configuration to the 302 ms condition of Honda's (2006) study (duration: 302 ms motion vs. 500 ms motion; configuration: 31 LEDs flashed successively at 10 ms intervals moving downward by 0.6° on each step for 18° of travel vs. 60 successive presentations of dot on a CRT at 8.33 ms intervals moving downward by 0.416° on each step to cover 25°). As in Honda's experiment, our probe's path was placed midway along and orthogonal to the saccade, so that the saccade produced a sharp lateral motion of the probe on the retina in the opposite direction of the saccade (Figure 2b).

To foreshadow our results, the moving probe when presented at low contrast was not seen to curve away from and then back toward its downward path; the pre-existing location information for the dot as it moved down the screen appeared to override any peri-saccadic mislocalization. Nevertheless, the trace appeared to be broken into two straight segments that did not line up, with the post-saccadic portion shifted in the saccade direction relative to the pre-saccadic portion (Figure 2e) consistent with our earlier result based on apparent motion (Szinte & Cavanagh, 2011). To measure the misalignment between the pre- and post-saccadic

Movie 1. Stimulus demonstration. Click on the video to make it start. Move your gaze to follow the jumping white dot. While moving your eyes, pay attention to the motion trajectory of the red square. The trajectory is best seen in a dark room on an otherwise dark monitor. Although the trajectory is straight, many observers (with uncontrolled display conditions) and all our participants in our experimental conditions, perceive two segments not one, with the earlier one seen offset horizontally from the second in the direction opposite to the saccade.

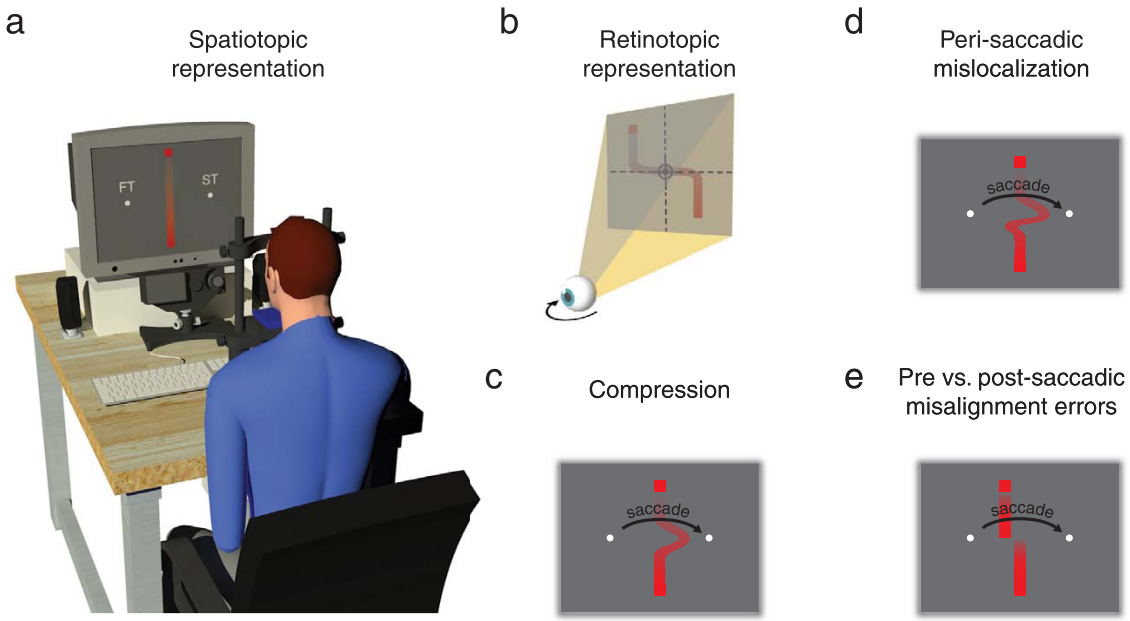


Figure 2. Visual representations. (a) Observers were instructed to saccade from a fixation target (FT) to a saccade target (ST) while a red square moved continuously downward. (b) On the retina, when observers performed a rightward saccade, the first part of the motion path falls to the right of the fovea while the second part falls to the left, crossing the fovea at the mid-point of the saccade. (c) From the prediction of the compression effect (Ross et al., 1997) the perceived motion should deviate toward the saccade target and then go back to the actual path just around the time of the saccade ("Compression"). (d) Peri-saccadic mislocalization literature will predict the same pre-saccadic effect but after the saccade the path should deviate toward the fixation target to then go back to the actual path. (e) Here, we observed that the motion appears as it is in space, with a systematic error of compensation leading to the perception of two motion traces that are horizontally misaligned ("pre vs. post-saccadic misalignment error").

segments, we introduced a blank in the central 200 ms bracketing the saccade. Then, to measure the timing of the break between the two segments, we presented the entire motion path with the appropriate counter-shift at different times relative to the saccade. This allowed us to evaluate the temporal dynamics of the shift by a simple report of motion continuity, and showed that the position compensation for the saccade occurred in time near the mid-point of the saccade itself. Finally, we increased the display contrast to be a better match to Honda's stimuli (2006), and found that the deviations around the time of the saccade became visible for some observers but the overall misalignment between pre- and post-saccadic segments remained as before.

Experiment 1

Materials and methods

Observers

Six volunteers from Université Paris Descartes took part in Experiment 1 (one author, and five observers naïve to the purpose of the experiment, age 21–31 years, three males and three females). All had normal or corrected-to-normal vision and gave informed consent. The experiments were carried out according to ethical standards specified in the Declaration of Helsinki.

Instruments and stimuli

Observers were seated in a quiet, dimly lit room with their head positioned on a chin rest 60 cm in front of a computer screen. The fixation markers were 0.6°-diameter white dots (68.0 cd/m^2) and the moving stimulus was a 1°-side red square (12.0 cd/m^2), all on a dark-gray background (4.5 cd/m^2), presented on a 22" Sony GMD-F520 screen (Sony, Tokyo, Japan) with a spatial resolution of 1,440 by 1,050 pixels (36.7° by 27.6°) and a vertical refresh rate of 120 Hz. The experiment was controlled by an Apple MacPro Dual Intel-Core Xeon computer (Apple, Inc., Cupertino, CA). The dominant eye's gaze position was recorded and available online using an EyeLink 1000 Desktop Mounted Eye Tracker (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 2 kHz. The experimental software controlling stimuli display and response collection was implemented in Matlab (MathWorks, Natick, MA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peter, & Palmer, 2002) toolboxes. Saccades were detected online when the gaze passed outside a virtual circle of 1.5°-radius centered on the fixation target and landed later within a second virtual circle of 2°-radius centered on the saccade target. Eye movement data were also re-analyzed offline based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006) computed from subsequent samples in the eye position series. The thresholds for peak velocity and minimum duration used for saccade detection were 3 SD and 20 ms. Psychometric functions were fitted using the Psignifit toolbox (Wichmann & Hill, 2001a, 2001b).

Procedure

Each trial began with a fixation target made of a white circle, filled with a smaller, dark gray bull's-eye. This fixation target was presented on the horizontal midline of the screen and could appear 7.5° to the right or to the left of screen center leading to an equiprobable number of 15° rightward and leftward saccade trials. When the participant's gaze was detected within a 1.5°-radius virtual circle centered on the fixation target, the bull's-eye changed from dark gray to orange. The orange dot indicated that fixation was achieved and that the next trial would start momentarily. After 400 ms of correct fixation the target was entirely filled with white and the trial began. After a random period of fixation between 300 and 1100 ms (five possible times separated by 200 ms), a red square (the visual probe) appeared at 12.5° above the horizontal midline of the screen. This square always moved downward for 500 ms at a constant speed of 50°/sec, covering a vertical amplitude of 25° (stepping ~0.42° per screen refresh).

In the first experiment, the horizontal position of the moving probe varied between trials but started close to the screen midline. The central 200 ms segment of the probe's motion was blanked (Figure 3a and Movie 2), creating two motion segments of 150 ms each (7.5° amplitude each, blanked over the central 10°). This procedure gave the impression that the square passed behind an object of the same color as the background without changing its speed. In order to trigger a saccade during this blank period we presented the saccade target and simultaneously extinguished the fixation target 25 ms after the probe appearance. Observers were asked to saccade to the new fixation location and, all the while, to pay attention to the probe motion. Thus, after the appearance of the saccade target, the probe kept moving downward for another 125 ms and was blanked for 200 ms, and then reappeared for 150 ms. Finally, 200 ms after the end of the motion sequence a red ring appeared around the saccade target indicating that the observers should then report whether the second motion trace (the one after the probe blanking) was more to the left or to the right of the first motion trace (the one before the probe blanking).

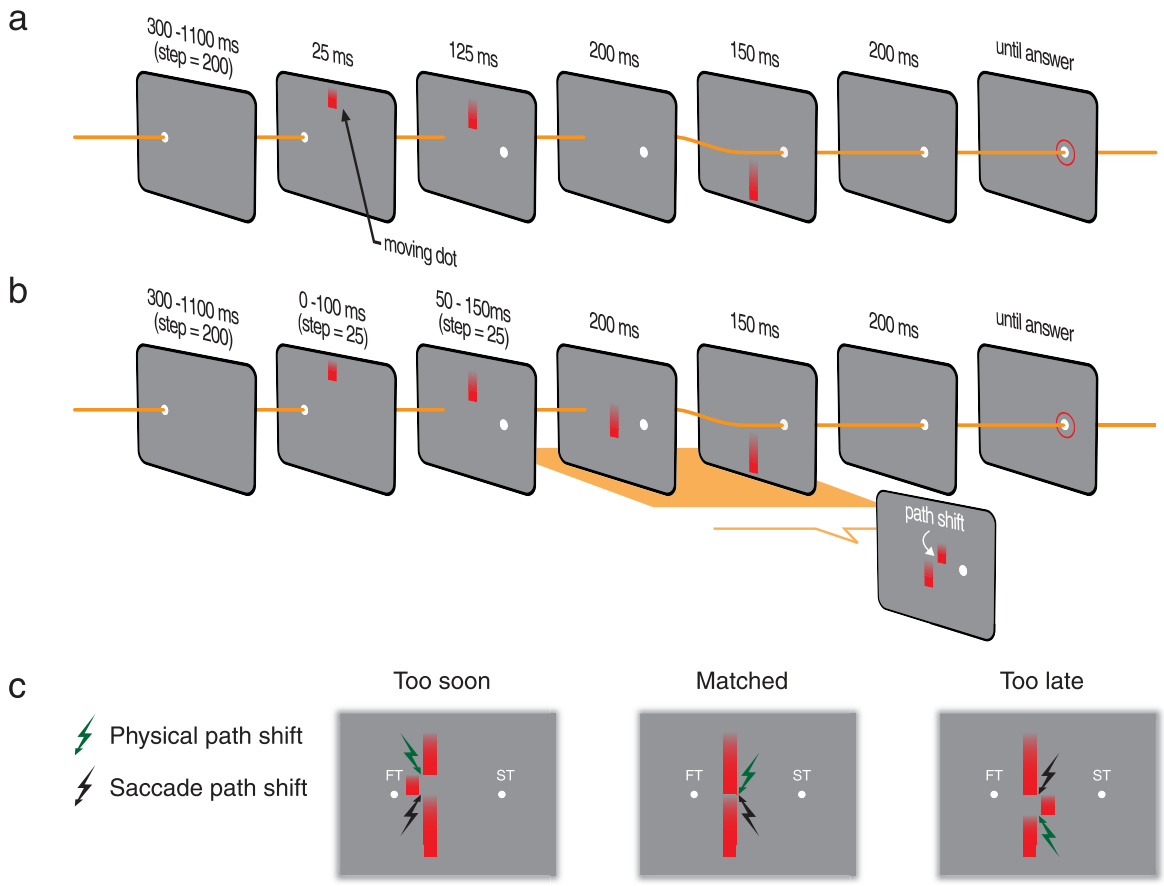
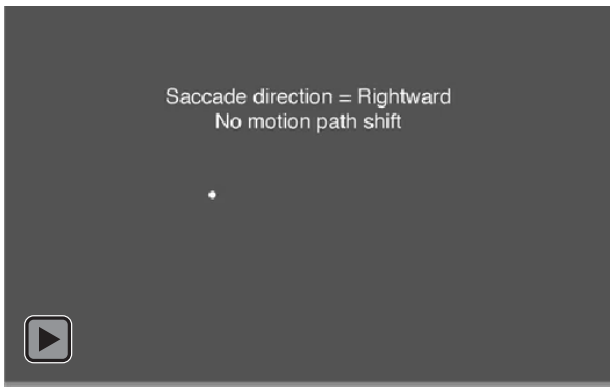


Figure 3. Stimulus sequences. The orange line represents the line of gaze during a rightward saccade trial. Shortly after the red dot began its downward motion, the white fixation spot jumped 15° to the right; observers were instructed to saccade rapidly to the new fixation location while simultaneously paying attention to the downward motion path. (a) In the first experiment, we measured the apparent offset between the pre- and post-saccadic vertical motion paths. A blank of 200 ms was inserted in the middle of the path to make any offset noticeable and easy to report. Observers reported whether they perceived the latter, lower motion trace (post-saccadic) to the left or right of the upper trace (pre-saccadic). (b) In the second experiment, we measured the time at which the offset occurred relative to the saccade. Observers again saccaded as soon as the white fixation dot shifted location. The downward motion of the red dot continued without blanking but its path was abruptly, physically shifted by the amount that should correct the pre- and post-saccadic misalignment, as measured in the first experiment. This physical path shift was introduced at different times relative to the saccade onset (orange area) and observers were asked to report whether the motion trace looked continuous or appeared to have breaks. (c) If the physical path shift preceded or followed the saccade-induced shift in time, observers saw two breaks ("Too soon" and "Too late"). The motion trace would be most likely to look continuous if the physical path shift matched the saccade-induced shift in both size and timing (see "Matched").

We used multiple staircases to adjust the horizontal gap between the first and the second motion traces so that the physical offset nulled the saccade-induced misalignment. In order to do so, the horizontal position of the top and bottom motion paths were offset simultaneously in opposite directions. In each experimental block we ran four simultaneous staircases of 40 or 60 trials each (two staircases for rightward and two for leftward saccade trials), starting successively at one of six randomly chosen horizontal offsets between top and bottom motion paths that were linearly spaced between +2° and −2° around the horizontal midpoint of the screen (negative values mean that the second motion trace was displayed to the left of the first one).

Trials were screened online based on the spatial properties of the saccade (started within 1.5° of the fixation target and ended within 2° of the saccade target) and the temporal properties (saccade should occur within the interval where the moving probe was blanked). Trials that didn't satisfy these criteria were randomly replaced later in the block and the trial



Movie 2. Stimuli from Experiment 1. This video contains three different examples of rightward saccade trials from the first experiment. First, fixate the white dot and press the play button on the bottom left corner of the movie. The red dot will start moving down the screen. Then, as soon as the white dot moves to the right, shift fixation to its new location. At the same time, notice whether the second, lower portion of the motion trace falls to the left or to the right of the initial, upper one. In the first sequence, both motion traces are aligned; in the second sequence, the second one is displaced in the opposite direction of the saccade (motion path shift: −13% of saccade size); in the third sequence the second motion trace is displaced in the direction of the saccade (motion path shift: +13% of saccade size).

outcome did not affect the current staircase. To familiarize observers with these criteria and with the task itself, they ran a block of 160 or 240 trials in which feedback on the saccade execution was given after each trial. No feedback was given during the experimental trials. The data obtained in the training blocks weren't taken into account for later analyses. Each observer ran the training block and three experimental blocks composed of 160 or 240 trials each (three observers ran 480 trials, the others ran 720 trials) in three different sessions. Each session was composed of one block and lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min.

Before proceeding to the behavioral analyses, we re-analyzed the fixation and saccade execution records following strict criteria (Results and Figure 4a). We then determined for each observer, and each saccade direction separately, the horizontal offset between motion traces that elicited the perception of two aligned traces. To do so we fitted cumulative Gaussian functions onto the proportion of "right" reports (i.e., the second, lower motion trace perceived to the right of the first, upper one) for each horizontal offset tested. We then determined the point of subjective alignment (PSA) corresponding to the level of 50% of "right" reports.

Results

In this first experiment, we evaluated the size of the horizontal offset between pre- and post-saccadic motion segments. To do so, we determined the horizontal offset between motion segments necessary for participants to perceive them as aligned across a saccade while masking the central portion of motion. Overall, 4,741 trials were run across all observers but of these, 901 were rejected online as falling outside the spatial and temporal criteria during the online analysis, leaving 3,840 selected trials. We then re-analyzed the eye-tracking data for these trials offline in order to keep those where observers' saccades were spatially accurate and fixation was maintained correctly throughout the 150 ms before and the 150 ms after the probe blank period (within a radius of 1.5° and 2° centered respectively on the fixation and the saccade target). This selection, added to the online detection of correctly timed saccades (during the probe blank), together with the rejection of blinks, allowed us to select trials during which the eye was steady for all of the 150 ms durations of both the pre- and post-saccadic motion traces. Across all observers, these offline analyses led us to reject a further 287 trials, leaving 92.5% of all trials selected online (3,553/3,840) and 74.9% of all trials (3,553/4,741). Figure 4a shows the outcome of the offline selection for the horizontal eye positions of 60 representative trials.

We plotted a psychometric function based on the reports from these correct trials to determine the perceived horizontal offset between the two motion traces. The offset at which "right" reports reached 50% defined the point of subjective alignment (PSA) where the pre- and post-saccadic traces appeared aligned. Psychometric curves for two representative observers and two directions of saccade are displayed in Figure 5a and the results observed for all observers are displayed in Figure 5b. Figure 5b shows that the perceived shift (opposite to the PSA that nulls it) of the pre-saccadic trace is in the direction opposite to the saccade. This is observed for each observer and direction of saccade as well as for the mean across all observers.

We found a main effect of the saccade direction on the PSAs ($F[1,5] = 14.69$, $p < 0.05$), confirming that the shift of the pre- versus post-saccadic trace is to the left for a rightward saccade and to the right for a leftward saccade. These observed biases imply that the corrections for the effect of the saccade on perceived location were too large (hypermetric or over-compensated). For example, the fitted curves for the first observer indicate PSAs of −4.24° ± 1.18° and +3.0° ± 0.35° for rightward and leftward trials, respectively, resulting an overcompensation of the saccade by about a quarter of the saccade amplitude. On all observers our results reflect a

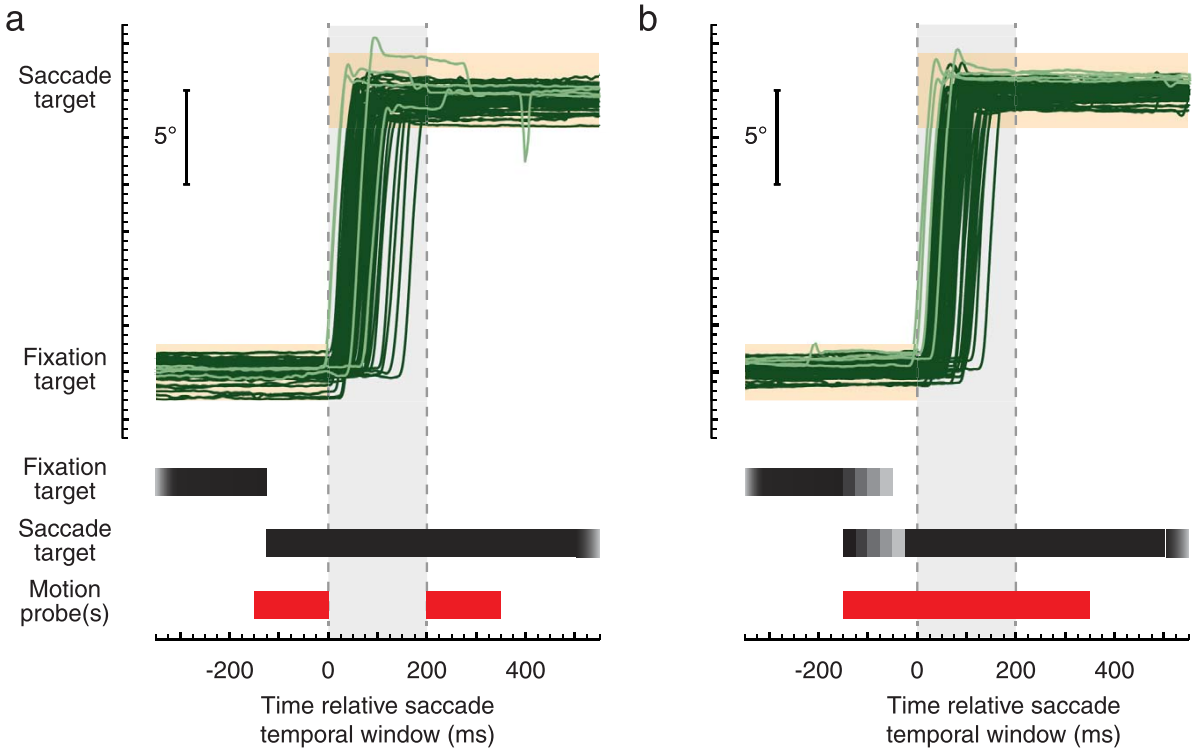


Figure 4. Trial selection. These graphs show 60 representative horizontal eye traces from all observers of the first (a) and the second experiment (b). In the first experiment, in order to select trials with saccades executed only within the 200 ms blank period, we used strict offline criteria (accurate fixation before and after saccade, correctly timed saccade, no blink, see text for more details) in addition to the online selection. We then kept the same criteria in the second experiment in order to compare similar saccade trial profiles. For both experiments, we sorted trials into two categories, "correct saccade" (dark green lines) and "incorrect saccade" trials (light green lines). Each "correct saccade" falls inside the saccade temporal window (gray area) and begins and ends within the acceptable pre- and post-saccadic spatial windows (light-orange areas). The bottom of each panel displays the presentations of the moving probe (red bars) as well as fixation and saccade targets (black bars). In Experiment 2, the saccade target could appear at different times relative to the saccade temporal window; these different timings are represented in the right panel by the different levels of gray in the fixation and saccade target bars.

systematic overcompensation of 23.6% of the saccade amplitude (error of 3.54° for saccades of 15°).

Conclusion

This first experiment demonstrated that the observers perceived the motion trace of the probe in roughly spatiotopic rather than retinotopic coordinates with, nevertheless, a systematic error of compensation suggesting an over-correction of approximately one-fifth to one-quarter of the saccade amplitude. These properties of the compensation processes are similar to those observed previously with trans-saccadic apparent motion (Szinte & Cavanagh, 2011). For the initial motion trace to been seen in its actual spatial location, the persisting image of the pre-saccadic trace must be reassigned to a location shifted in the direction opposite to that of the saccade by an amount equal to the saccade amplitude. Participants did not report seeing anything other than straight motion traces before and after the blanked out segment around the time of the saccade but that is to be expected given that the moving stimulus was not visible during the critical 200 ms before and after the saccade where compression is seen (Ross et al., 1997). The blanking allowed us to measure a baseline shift of the pre- vs. post-saccadic localization but also hid the path of remapping right around the time of the saccade.

Experiment 2

In our first experiment, we had evaluated the size of the horizontal offset between pre- and post-saccadic

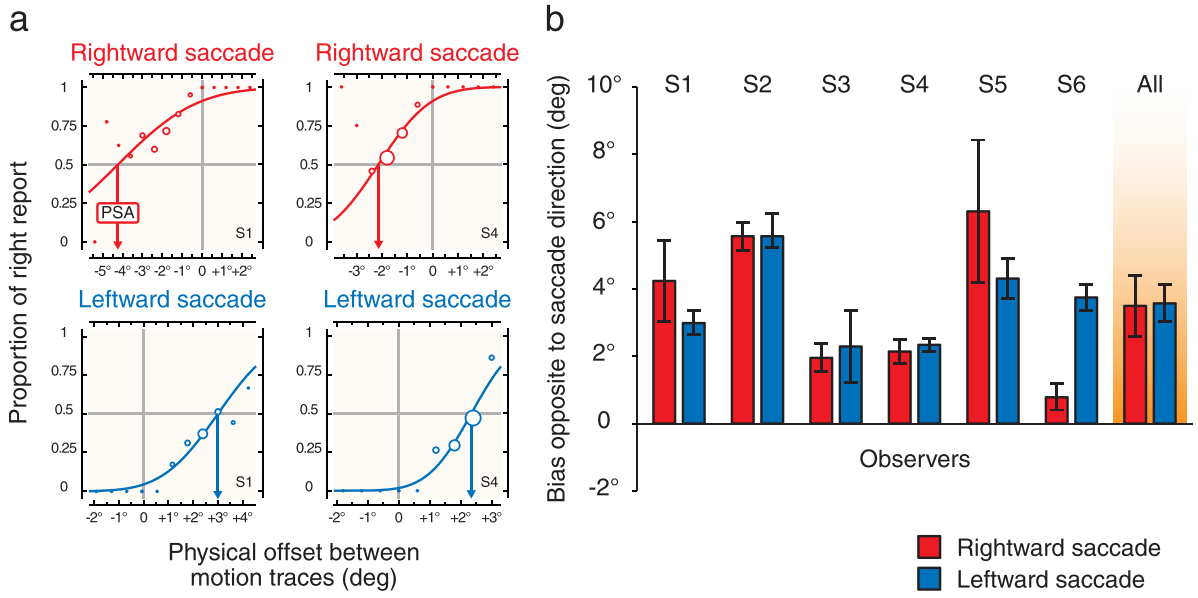


Figure 5. Individual and group results of Experiment 1. (a) Proportion of "right" report in function of the physical offset presented between motion trace, for two representative observers for rightward (red curves) and leftward (blue curves) "correct saccade" trials. Psychometric functions were fitted to estimate the point of subjective alignment (PSA), i.e., the amount of horizontal physical offset between motion traces leading to equal response of "right" or "left" shift of the second motion trace relative to the first one. (b) Results for all observers and for the group. Bars represent the measured bias in the opposite direction of the saccade for each observers and saccade directions individually as well as the average across observers. Errors bars for each observer indicate 95% confidence interval computed by bootstrapping and the *SEM* for all observers.

segments of motion. This measure was used in this second experiment in order to cancel the offset and determine the timing of the perceived shift, if any.

Materials and methods

Observers, instruments, and stimuli

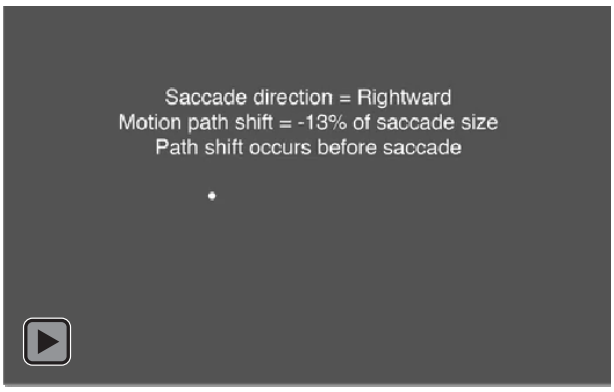
The observers, instruments and stimuli were the same as for the first experiment.

Procedure

The procedure for the second experiment was the same as for the first with the following exceptions. First, the moving dot continued in motion over its 25° path without being blanked. It was, however, offset at a particular moment during its descent. The shift that made the two segments appear aligned for each observer in Experiment 1 was now introduced at various time points during its descent (Figure 3b and Movie 3).

To trigger saccades at different times relative to the probe shift, we presented the saccade target simultaneously with the disappearance of the fixation target at five random times between 0 and 100 ms (separated by 25 ms each) after the red dot began its downward motion. Using a method of constant stimuli we inserted the physical shift of the probe path equiprobable at one of 13 times between 100 ms and 400 ms after the probe appearance. Seven of these time points for the probe shift were distributed evenly between 100 ms and 400 ms (separated by step of 50 ms) after the probe appeared and began to move. To increase our sampling at the time of the saccade, we added six more time points at 8 ms intervals locked to the online detection of the saccade (average delay from detection to first probe shift was 14 ms ± 3 ms). Finally, 200 ms after the end of the motion sequence a red ring appeared around the saccade target indicating that observers should report whether the motion trace looked continuous, that is with or without break. We instructed observers to use the "continuous" response only if they saw an unbroken, straight motion trace.

We determined the correct execution of saccades online using the same criteria as in the first experiment and replayed randomly trials that did not satisfied these criterions. Each observer ran 20 experimental blocks of 26 correct trials each (520 correct trials), composed of equiprobable rightward and leftward saccade trials for the 13 possible times of the probe shift. Each observer ran four sessions composed of five blocks each that



Movie 3. Stimuli from Experiment 2. This video contains three different examples of rightward saccade trials from the second experiment. First, fixate the white dot and press the play button on the bottom left corner of the movie. The red dot will start moving down the screen. Then, as soon as the white dot moves to the right, shift fixation to its new location. At the same time, judge whether the motion trace looked continuous or not. In the first sequence the motion path shifts before the saccade target appears so two breaks should be seen: the physical shift followed by the saccade-induced shift; in the second sequence, the motion shift is presented around the time of a typical saccade and in this case the two shifts might cancel although this typically would require more exact matching of shift size and timing; finally, in the third sequence, the motion shift is presented long after the saccade target so that again, two shifts should be seen, in this case the saccade-induced shift followed by the physical shift. For these examples we used a motion shift of 13% of the saccade amplitude in the direction opposite to the saccade.

lasted less than 25 min each. During each session, the eye-tracking system was recalibrated every 8 min. Before proceeding to the behavioral analyses, we further screened the trials based on more stringent spatial and temporal criteria (Results and Figure 4b).

Results

We presented the moving dot before, during, and after the saccade so that any deviations occurring closer to the saccade could be seen. To determine if there was any deviation of the trajectory as might be predicted from the compression or peri-saccadic mislocalization results (Figure 2c-d), we asked observers to report if the trajectory appeared to be a continuous, linear trace. We already knew from Experiment 1 that the beginning and ending segments appeared misaligned, so we corrected the trajectory with a horizontal offset matched to each observer's measured offset. If there were major deviations corresponding to the compression or peri-saccadic mislocalization results, observers would never report a continuous linear path. However, only breaks between linear segments were reported by participants. If the physical shift preceded or followed the saccade-induced shift in time, the participants saw two breaks, with the trace shifted first one way, and then back to the aligned beginning and end segments of the trace (Figure 3c, "too soon" or "too late"). The impression of continuous motion with no break required that the physical shift occurred at roughly the same time as (and in the opposite direction to) the saccade-induced shift (Figure 3c, "Matched"). In that case, all participants frequently reported seeing a continuous, linear trace. Depending on the observer, the maximum frequency at the peak of the Gaussian fit reached from 71% to 100% of trials at the optimal timing, with a mean maximum frequency of continuity reports at optimal timing of 85% ± 3%.

We determined for each participant and saccade direction the proportion of continuity reports of the motion trace for the different times of the physical shift latency relative to the saccade onset (in bins of 10 ms). We then evaluated the mean as well as the confidence interval of a normal Gaussian function fitted to the data. To take into account the different number of trials in each bin, we weighted the fit of the Gaussian by the number of trials that had been averaged into each datum point. The online analysis of the saccade led to rejection of 18.0% (683/3,803) of all trials as inaccurate, leaving 3,120 accepted trials. We then re-analyzed these accepted trials offline following the same stringent spatial and temporal criteria as in Experiment 1. We use the same temporal criteria, requiring saccade to be executed during the central 200 ms of the moving probe, corresponding to the blank period of Experiment 1, which now was not blank. Figure 4b displays the horizontal eye positions of 60 representative trials synchronized to the saccade temporal window onset. Across all observers these offline analyses led us to keep 92.7% of all trials selected online (2,891/3,120), corresponding to 76% of all trials (2,891/3,803).

Figure 6a displays, for two representative observers and for the two directions of saccade, the distributions of the continuity reports across different timings of the corrective shift relative to the saccade onset. For example, for the first observer with rightward saccades (upper left panel in Figure 6a), the maximum frequency of continuity reports occurs at 21.4 ± 5.7 ms after the saccade onset. This means that if the probe motion is presented 21 ms after the saccade onset with a horizontal shift of 4.24° in the opposite direction of the saccade (this observer's bias), then this observer reported seeing the probe move continuously down the screen more frequently than at any other timing, seeing no breaks or deviations in the motion trace. For each observer we determined the mean and the confidence interval of these Gaussian distributions and these values are shown in Figure 6b as well as the average

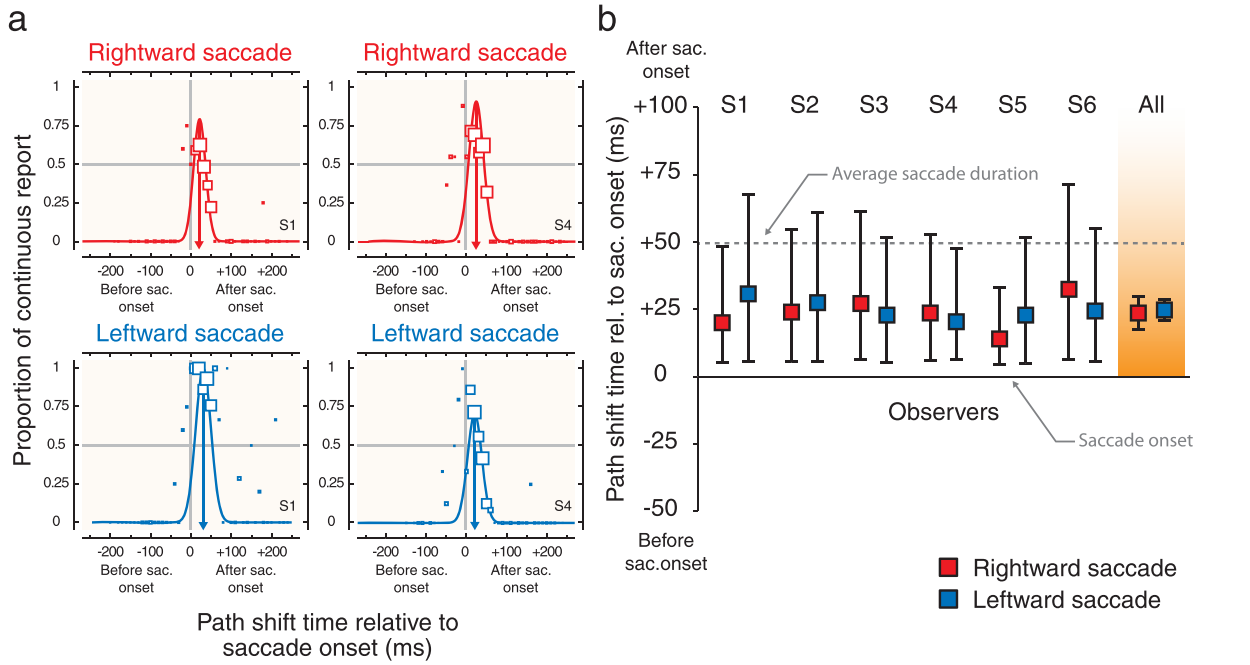


Figure 6. Individual and group results of Experiment 2. (a) Proportion of "continuous" motion reports as a function of the time of the motion path shift relative to the saccade onset, for two representative observers for rightward (red lines) and leftward (blue lines) "correct saccade" trials. The Gaussian functions fitting these data are weighted by the number of observations per bin. (b) Timing of maximum frequency of "continuous" reports (peaks of fitted Gaussians) for each observer and saccade direction and for the group. Error bars for individual observers indicate 95% confidence interval of the Gaussian distributions and the *SEM* for all observers.

across all observers. Results were highly similar across participants ($F[5,5] = 0.88$, $p = 0.55$) and no significant difference was observed between the two saccade directions tested ($F[1,5] = 0.13$, $p = 0.73$). Across observers and saccade directions, the peak frequency of continuity reports occurred at 24.4 ± 1.6 ms after the saccade onset. As illustrated in Figure 6b (see gray dashed line), the mean saccade duration was 48.9 ± 2.1 ms (median: 48.17 ± 2.1 ms), and no significant differences were observed for the mean or median saccade duration between participants (for the mean saccade duration: $F[5,5] = 2.92$, $p = 0.13$; for the median saccade duration: $F[5,5] = 2.49$, $p = 0.17$) or saccade directions (mean: $F[1,5] = 0.20$, $p = 0.67$; median: $F[1,5] = 0.09$, $p = 0.78$). The moment at which the pre-saccadic trace shifts therefore falls during the saccade flight, suggesting that at a perceptual level the compensation is in place when the saccade lands.

Conclusion

By presenting a physical offset in the motion path that nulled the error in saccade compensation, we were able to determine the moment at which the persisting pre-saccadic motion trace is shifted to its (almost) appropriate spatiotopic location. Our results suggest that this process occurs at about 24 ms after saccade onset and that once this is corrected, no other deviations in the path were seen. That is, no deviations were reported that would correspond either to the large peri-saccadic mislocalization seen with single flashes (Honda, 1989; Matin & Pearce, 1965; Ross et al., 1997) or the small deviations previously reported by Honda (2006) in a similar moving probe design. However, these deviations of the visible motion may be masked by saccadic suppression (Burr, Holt, Johnstone, & Ross, 1982; Matin, 1974) and might be revealed at higher contrasts, a question we investigate in the next experiment. We also emphasize that the shift of the pre-saccadic portion of the trace is a repositioning of the entire persisting trace. It is this repositioned trace that has the linear feature that observers use to report the alignment or misalignment of the pre- and post-saccadic segments. Our data do not specify the duration of this repositioning, it may well start before the saccade and end after, we can only determine its midpoint, which is near the middle of the saccade. The position of the pre-saccadic motion trace can be reported both before and after the saccade, but there appears to be no experience of its displacement between these locations even though this entails a shift of several

degrees. As is the case for deviations of the moving dot itself around the time of the saccade, the visibility of this shift of the entire pre-saccadic motion trace may also be suppressed by the saccade.

Experiment 3

Results from Experiments 1 and 2 suggest that pre- and post-saccadic motion traces were seen as misaligned and that the pre-saccadic segment was mislocalized in the direction opposite to the saccade, relative to the post-saccadic segment, by approximately one-fifth of the saccade amplitude. In contrast, Honda's observers reported (by making drawings) that the pre- and post-saccadic trajectories were *aligned* and showed as well a small deviation at the time of the saccade (Figure 1). We therefore ran a final experiment to examine the effect of the remaining differences between our stimuli and Honda's: saccade target duration (in his case the saccade target stayed on during 20 ms, in ours, it stayed until the end of the trials, so for at least 600 ms); and the contrast of the moving probes (in his case 30 cd/m^2 on black background; in ours, 12 cd/m^2 on a background of 4.5 cd/m^2). We changed our display to match these values as closely as possible and asked observers to report the relative horizontal difference (if any) of the pre- and post-saccadic motion traces. They did so, after the probe motion was finished, by moving two vertical lines to mimic the alignment they had seen. Also, at the end of the session, we asked them to draw the perceived trajectory as Honda did.

Materials and methods

Observers, instruments, and stimuli

Five volunteers from Université Paris Descartes took part in Experiment 3 (one author and four observers naïve to the purpose of the experiment, ages 22–37, four males and one female, two of who had participated in Experiments 1 and 2). All had normal or corrected-to-normal vision and gave informed consent. The experiments were carried out according to ethical standards specified in the Declaration of Helsinki.

The instruments and stimuli were the same as before except that the screen background was either black (0.1 cd/m^2) or dark-gray (4.5 cd/m^2). In the black screen background condition, we turned off the experimenter screen (eye-tracking control screen) in order to limit the external lights to the eye-tracker infrared lights and to the dim background of the CRT screen. Finally, saccades were detected online and re-analyzed offline using the same criteria as Experiments 1 and 2.

Procedure

The procedure for the first part of this experiment was the same as for Experiments 1 and 2 with the following exceptions. First, the probe contrast was increased on all trials by reducing the luminance of the screen background, from dark-gray to black. Second, although the duration of the fixation target, and probe were the same as in Experiment 1 (Figure 3a), the saccade target was either presented until the end of the trial (as in Experiments 1 and 2) or lasted only three monitor frames (25 ms, compared to 20 ms for Honda, 2006) leading respectively to "visible target" and "memory target" saccade trials which were equal in number and randomly intermixed. Next, the moving dot could either be continuously presented over its 25° path (as it was in Experiment 2 and Honda's experiments) or blanked in its central part (as it was in Experiment 1) leading to equal numbers of "blanked" and "continuous" motion trials in a random sequence. Moreover, contrary to Experiments 1 and 2, the motion probe always followed a continuous trajectory, directly down the display at the screen center without any shift in the path. At the end of each trial, we asked observers to report the horizontal offset between the top and bottom motion traces by adjusting with a computer mouse the horizontal location of two bars (7.5° by 1° each, 5° above and below the screen center, 1 cd/m^2) presented sequentially at a random horizontal location between +3° and −3° around screen center. As before, saccades were screened online and trials that didn't satisfy our criteria were randomly replaced later. In order to be familiarized with our criteria and the task itself, observers ran a session of 80 trials in which feedback on the saccade execution was given. No feedback was given during the experimental trials. The data obtained in the training session weren't taken into account for later analyses. Each observer ran the training session and three experimental sessions composed of 80 trials each. Each session lasted less than 20 min. During each session, the eye-tracking system was recalibrated every 8 min.

Finally, after these adjustment trials, in the second part of the experiment, observers were presented a series of "drawing" trials with continuous motion of the probe where no adjustment responses were made. The observers were asked to focus on the whole motion trajectory and instructed to remember the perceived motion traces that they would later draw without having their head on the chin rest. We presented the trials in four blocks in random order. Each block had 15 identical trials composed of either rightward or leftward saccade trials and with contrast and saccade target similar either to our first and second experiments ("low contrast motion," red probe on dark-gray background, visible target saccade) or to Honda's experiments ("high contrast motion," red probe on

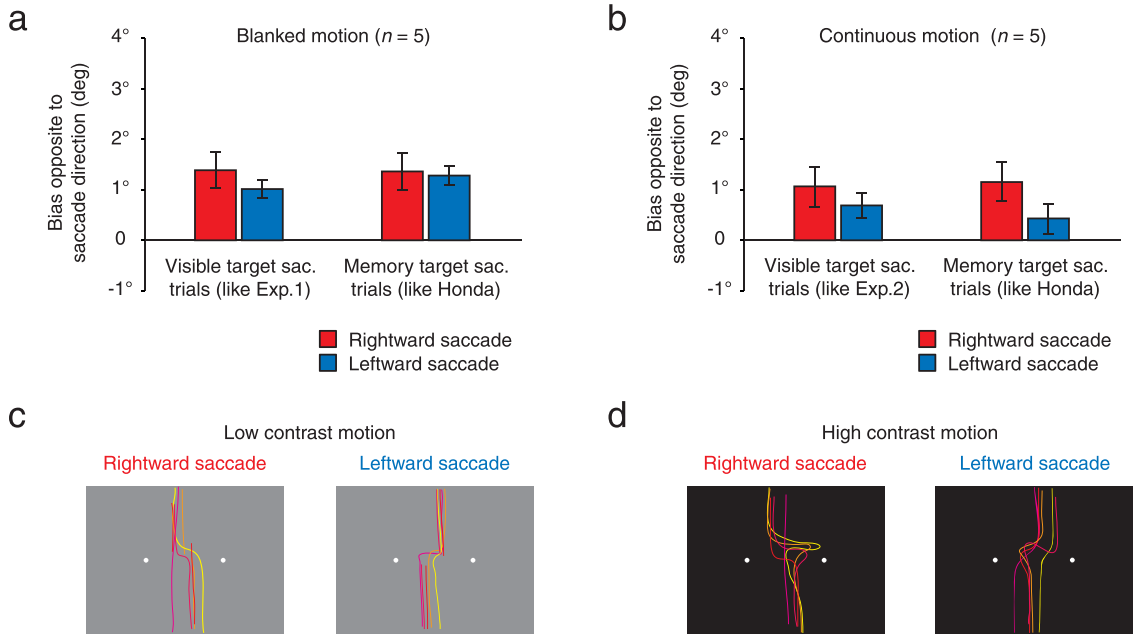


Figure 7. Group results of Experiment 3. (a) Bars represent the measured bias in the direction opposite that of the saccade, averaged across observers (n = 5) in the "visible target" saccade trials (like those of Experiment 1) and the "memory target" saccade trials (like those of Honda, 2006). Errors bars indicate the *SEM*. (b) Same observations for the continuous motion condition for the "gap saccade" trials (like those of Experiment 2) and the "memory saccade" trials (like those of Honda, 2006). Errors bars indicate the *SEM*. (c) This panel shows 10 representative drawings made by the observers in the low-contrast motion case in rightward and leftward saccade trials. The line colors from magenta to yellow are present to visually segment the reported traces. (d) Same observations for the high-contrast motion condition.

black background, memory target saccade). At the end of each block, observers drew five trials that they consider as the most representative of the 15 trials they had seen. Saccades were screened online and trials that did not satisfy our criteria were randomly replaced later. Feedback was given after each incorrect saccade trial and observers were instructed to ignore those trials in their later drawings. Drawings were collected on an electronic tablet using an electronic pencil and a drawing software (SketchBookPro for iPad, Autodesk, San Rafael, CA), saccade as well as fixation targets were presented on the drawing display and observers were familiarized with the device before running the experiment.

Results

We used the same online and offline saccade analysis as in Experiments 1 and 2. The online analysis rejected 25.7% (415/1,615) of the trials and the offline analyses rejected a further 11.4%, leaving 1,063 trials. Figures 7a and 7b show the average setting of offset between upper and lower bars for the "blanked" (moving probe not shown in middle 200 ms) and "continuous" (probe always present) conditions, respectively. The size of the offset did not differ between "blanked" and "continuous" trials (two-tailed t-test, $t(4) = 2.571$, $p = 0.07$). In both cases, the pre-saccadic segment was seen shifted in the direction opposite to the saccade (relative to the post-saccadic segment). These results are consistent with the findings in Experiments 1 and 2, despite the differences in background contrast and measurement procedure.

More specifically in the blanked condition the pre-saccadic trace was on average perceived shifted 1.27° ± 0.09° in the opposite direction to the saccade. Within those trials there were no significant differences between saccade directions ($F[1,12] = 1.011$, $p = 0.33$), or target durations (visible or memory saccade trials: $F[1,12] = 0.279$, $p = 0.61$) nor a significant interaction between these two factors ($F[1,12] = 0.446$, $p = 0.52$).

In the continuous condition, the pre-saccadic trace is on average perceived shifted 0.84° ± 0.17° in the opposite direction to the saccade. Again there was no significant difference between saccade directions ($F(1,12) = 1.895$, $p = 0.19$), saccade target durations ($F(1,12) = 0.051$, $p = 0.82$) and no significant interaction between them ($F(1,12) = 0.183$, $p = 0.68$).

Making the stimulus parameters closer to Honda's did, however, affect the perceived trace right around the time of the saccade (in the continuous condition). Here, the drawings of observers showed that some observers (two of five) saw in some trials a deviation in the trace, when the probe had high contrast but never at low contrast. However, even when the excursion was reported, observers do not see an alignment between the top and bottom motion trace as can be observed in Figure 7d. Even in these drawings with a visible peri-saccadic excursion in the trace, observers still report an offset between pre- and post-saccadic segments that is similar in direction and amplitude to that measured just before with the alignment test.

Finally, it is interesting to note that with the higher contrast (and a different method of measurement), the measured biases were smaller than those from Experiment 1. This suggests that drawing attention to the path of the peri-saccadic motion trace might distract attention from the misalignment judgment, making it the less noticeable (a kind of change blindness).

Conclusion

These results demonstrated again that when a saccade occurs while an object is moving, the motion path does not conform to the path the object takes across the retina. Instead, it is perceived in roughly spatial coordinates, with, however, a systematic over-compensation of the saccade amplitude. This misalignment is seen in all of our experiments. In Experiment 3 with higher contrast, some observers also reported a deviation in the path around the time of the saccade, recovering one aspect of the findings in Honda's (2006) paper that was not reported by our observers with the lower contrast probe used in Experiment 2. Since the speed on the retina during the saccade is quite fast, it is reasonable that the deviations of the low-contrast probe in Experiment 2 might be missed, especially as it would occur during the interval of maximum saccadic suppression (Burr et al., 1982; Matin, 1974). Despite the visibility of the peri-saccadic excursion at high contrast, our observers, unlike Honda's, still reported the misalignment of the pre- and post-saccadic segments.

General discussion

We used a probe that moved on a linear path before, during, and after a saccade to visualize the dynamics of saccade compensation. The pre-saccadic portion of the trace was not seen to jump in the direction of the saccade as it does on the retina (Figure 2b); nor did it make a curve toward the saccade target and then back to the spatial path (Figure 2c) as would be expected from peri-saccadic compression (Ross et al., 1997) or a three-part curve (Figure 2d) as expected from peri-saccadic mislocalization (Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). Instead, the continuous motion trace was seen as two misaligned but linear segments, with the pre-saccadic segment shifted in the direction opposite to the saccade (Figure 2e). This first observation also differed from an earlier report by Honda (2006) using a similar moving probe technique. His observers, using drawing as a measure, reported that the pre- and post-saccadic segments appeared generally aligned and had, in some cases, a small, brief excursion at the time of the saccade. When we increased the contrast of our moving probe, some of our observers did report small excursions around the time of the saccade but even so, all our observers continued to see the pre- versus post-saccadic misalignment. We conclude that the moving probe does not provide any better access to fine-scale peri-saccadic mislocalization than a static flickering probe—that is to say, almost none at all. Apparently, the continuous, pre-existing position reference provided by the moving probe overrides any mislocalization that would be suffered by individual flashes or by flash sequences or motion traces beginning before the saccade (Sogo & Osaka, 2001; Watanabe et al., 2005). Nevertheless, the moving trace does reveal a large-scale mislocalization only previously reported in an apparent motion procedure (Szinte & Cavanagh, 2011) and it does so consistently across three different experimental procedures.

To characterize the timing and magnitude of this trans-saccadic misalignment, we first determined the horizontal offset between the pre- and post-saccadic segment of the moving probe while the central segment was blanked. In our procedure measurements were always made by relative judgments of the post- against the pre-saccadic trace. When the motion trace was actually aligned along its entire length, observers saw the pre-saccadic segment as shifted relative to the post-saccadic segment (shifted in the direction opposite that of the saccade). To bring the two segments into alignment, observers had to physically shift the post-saccadic segment, also in the direction opposite that of the saccade, by approximately one-fifth of the saccade amplitude (about 18° compensation for a 15° saccade). This result indicated that the pre-saccadic motion trace was corrected for the effect of the saccade and perceived in roughly spatiotopic rather than retinotopic coordinates. An accurate correction would have shifted the pre-saccadic trace by the entire length of the saccade; however, the effect of the saccade was overcompensated (hypermetric), moving the pre-saccadic trace too far.

We then introduced a horizontal shift in the continuous trace to cancel the over-correction and asked observers to report if the motion trajectory appeared to be a continuous linear trace or not. If the moving probe were physically offset at roughly the same time as the saccade-induced shift, observers would have an impression of continuity (if no other deviations from linearity were caused by the saccade). By evaluating the time profile of the continuity reports we identified the moment at which the pre-saccadic trace was shifted to its appropriate, nearly spatiotopic location. We found that this process occurs at about the midpoint of the saccade, suggesting that at a perceptual level the compensation is in place when the saccade lands.

We finally compared our results to a study reporting no misalignment between the pre- and post-saccadic trace (Honda, 2006). However, even with settings similar to those used in Honda's study, we still found the same misalignment. This misalignment remained even at high probe contrast when the peri-saccadic excursion that Honda had reported became visible.

How could we explain the perceived motion shift?

Perceptually, the pre-saccadic half of the motion trace is seen shifted, relative to the post-saccadic half, in the direction opposite to that of the saccade (Movie 1). However, this is a relative judgment that cannot assess whether the first, second or both segments shifted. It would seem that logically the shift should be attributed to the pre-saccadic trace, which needs to be corrected in order to appear relatively near its true spatial location; the second, continuing segment motion should be seen at the location corresponding to its retinal position as is the rest of the experimental scene. We have used the term "remapping" (Duhamel et al., 1992) to describe this correction of the pre-saccadic segment. Physiologic remapping is described as an anticipatory response in cells that will receive the target input after the saccade and the perceived correction of location in our experiments here may well be mediated by physiologic remapping. However, our experiment does not test any link between the physiologic remapping and our behavioral measures. Nevertheless, our results of an overcompensation may provide such a link if similar deviations in the location of remapping activity are found in single cell recordings. In addition to the amount and direction of the spatial correction, our results also offer a temporal profile of the correction and localize it to the midpoint of the saccade itself. The distribution of timings we see do extend before and after the saccade, as does the remapping activity (Duhamel et al., 1992; Goldberg & Bruce, 1990; Kusunoki & Goldberg, 2003; Umeno & Goldberg, 1997) although given the many factors that contribute to the shape of our "continuity" reports we do not place much weight on this.

This "remapping" correction is based on efference copy (von Holst & Mittelstaedt, 1950), an oculomotor command signal that, depending on the theory, acts on the whole visual field to detect and correct any change (von Helmholtz, 1867), or acts on a limited number of attended targets (Cavanagh et al., 2010; Wurtz, 2008), or is used to generate a spatiotopic map (Bischof and Kramer, 1968; Breitmeyer et al., 1982). An alternative mechanism to achieve visual constancy, the "reference object" theory (Bridgeman, 2007; Bridgeman, Van der Heijden, & Velichkovsky, 1994), operates post-saccadically, comparing a memory of the saccade target to the post-saccadic configuration to locate the original saccade goal and shift spatial coordinates to align with it. However, our results here suggested that the compensation of coordinates is already in place by the end of the saccade, giving little time for a "reference object" process to operate. Nevertheless, given that perception occurs with a substantial delay, this backdating of the correction is not a significant challenge to the reference object theory.

Whatever the mechanism producing the correction, we found a consistent error that was visible as a misalignment of the pre- and post-saccadic segments of the motion trace. Interestingly, this consistent error does not seem to be attenuated over time even though a mismatch between the expected and actual post-saccadic locations typically leads to rapid adaptation that minimizes this offset (Collins, Rolfs, Deubel, & Cavanagh, 2009). This saccadic adaptation effect is classically found for the saccade target itself whereas our target of interest was midway between the saccade goal and fixation. We should also point out, the adaptation is seen by many, though not all (Awater, Burr, Lappe, Morrone, & Goldberg, 2005), as a change in the motor response, not perception. Although these may be reasons for the absence of adaptation of the perceived locations in our experiments, another is that this persistent trans-saccadic shift has different values at different locations in the visual field (Szinte & Cavanagh, 2011), being an overcompensation at some locations and an undercompensation at others. These location-specific biases were quite stable over time in that earlier experiment and that raises the issue that not all of these shifts can be corrected by a common factor, and the remaining shifts may be the residual after the common factor is removed. However, since we tested the visible shift only at one location in this experiment, we cannot make any generalizations.

The timing of the shift, measured in our second experiment, appears to fall directly in the middle of the saccade itself, although this result specified only the time of the midpoint of the correction process, not its

duration. In that second experiment, we added a physical shift to offset the saccade-induced shift, and we based the size of this correction on the shift measured when there was a large gap in the central portion of the path (from Experiment 1). It is certainly possible that the size of the saccade-induced shift might be affected by the presence of that gap. In particular, Deubel and colleagues (1996) showed that adding a blank after the saccade improves the detection of a displacement of the saccade target. Nevertheless, the frequency of continuity reports reached extremely high values at the optimal timing (85% on average) suggesting that the amplitude of the correction that we used was appropriate and that the gap in the motion path did not affect the amount of perceived shift.

We might be concerned in the conditions with continuous motion traces (Experiment 2) that saccadic suppression (Bridgeman, Hendry, & Stark, 1975; Burr, Holt, Johnstone, & Ross, 1982; Matin, 1974) might mask the visibility of any displacements such as the physical path shift that we introduced into the trajectory near the time of the saccade and so account for the reports of continuity. In particular, when the physical step occurred very near the time of the saccade, its combination with the saccade-induced shift might produce a complex path that would not be seen because of saccadic suppression. It may well be smoothed out or filled in (see drawings). Despite the possible loss of details right around the time of the saccade, it is nevertheless clear that to cancel the otherwise visible saccade-induced shift, the physical counter-shift should be placed at or near the moment of the saccade itself. The physical shift and the uncorrected saccade shift became visible as soon as the physical shift occurred 50 ms before or after the saccade, indicating that the saccade-induced shift must be occurring within that window. Although saccadic suppression may obscure the details of the motion trace and its correction right around the time of the saccade, it does not suppress the misalignment seen between pre- and post-saccadic segments. These segments extend well beyond the range of saccadic suppression and when the pre- and the post-saccadic motion traces were actually aligned, saccadic suppression did not prevent our observers from seeing a displacement in the path.

Monitor persistence, retinal motion, and foveal bias factors

Could the observers' reports of a motion trace almost aligned in spatial coordinates (rather than retinal) have been a result of monitor persistence (Jonides, Irwin, & Yantis, 1982, 1983)? Clearly not, as any persisting trace on the monitor would have to be aligned over its whole length, independently of the saccade, a result that our observers never reported. Nor did retinal persistence appear to play any role as the retinal trace of the pre-saccadic motion path would be moved to the other side of the saccade target where it was never observed.

Could the retinal motion of the visual probe during the saccade contribute to the shift of the pre-saccadic trace and or its misalignment? Retinal motion of the probe could not be a factor in Experiment 1 where the probe was not present during saccade. Moreover, there was no effect of presence or absence of the probe during the saccade in Experiment 3 (blanked vs. continuous conditions). Overall, we have no evidence of that the probe's motion over the retina during the saccade contributes to the under-correction or over-correction of pre-saccadic locations.

Finally, we cannot entirely exclude the role of foveal bias (Mateeff & Gourevich, 1983; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999) where brief duration stimuli are seen closer to the fovea than long duration stimuli. If our pre-saccadic and post-saccadic probes are both seen closer to the fovea's location at the time of their presentation, this could, given a few other assumptions, mimic the direction of our effects. However, foveal bias has been reported only for briefly flashed, static stimuli whereas our moving probes were present for 150 ms (Experiments 1 & 3, blanked condition) or about 250 ms (Experiment 2 and the continuous condition of Experiment 3) before and after the saccade. In a previous study where we assessed the contribution of foveal bias directly for a trans-saccadic apparent motion stimulus, we found that it could explain no more than 20% of the pre- vs. post-saccadic misalignment (Szinte & Cavanagh, 2011).

What about mislocalization and compression?

In contrast to our pre- vs. post-saccadic misalignment (10% to 20% of saccade amplitude) and small peri-saccadic excursions (seen by some observers in Experiment 3), peri-saccadic mislocalization and compression effects (Lappe et al., 2000; Matin & Pearce, 1965; Ross et al., 1997) can be as large as the saccade itself. In these studies, a single, brief probe was presented around the time of the saccade and participants reported the perceived location of the probe after making the saccade. When the probe is located between fixation and the saccade target, it will appear increasingly shifted toward the saccade target in the 100 ms preceding the saccade, to be then shifted back in the opposite direction, returning to its veridical spatial location by about 100 ms after the saccade for the compression literature (Figure 2c), while for peri-saccadic mislocalization (Figure 2d), the path after the

saccade should deviate back toward the fixation target before returning to the actual path (Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). If any of these processes acted on our moving probe, it should have been seen to deviate toward the saccade target just prior to the saccade to then return to the veridical path just after it (Figure 2c) or after an opposite deviation toward the fixation (Figure 2d). The duration of this excursion would take up 20% to 40% of our motion path and so it would be difficult to miss in our continuous trace condition.

The critical difference between the two tasks is that, in our case, the probe is continuously present whereas in mislocalization and compression tasks, there is only a single, brief probe. It is possible that our continuous stimulus provides a reference for each new, slightly shifted point in the motion path, providing a landmark to stabilize the perceived location across the saccade. For example, Schlag and Schlag-Rey (1995) reported that a single point of light was seen as a streak if presented only during the saccade, but was stable and well localized if its presentation extended before or after the saccade. Honda (2006) also reported that largest mislocalization occurred when motion occurred right around the time of the saccade and found that little or no peri-saccadic mislocalization and compression when the duration of probe's motion extended before or after the saccade by 100 ms or more. Thus the stable location information of a continuously present, flickering probe appears to override the labile position information of the brief flashes and this effect of "grandfathering in" for well-defined position appears to hold for a moving probe as well, where the position, although changing, is predictable from one moment to the next.

However, this "grandfathering" effect did not override the large-scale misalignment (large-scale in terms of time, pre- vs. post-saccadic). Nor did any "filling-in" or saccadic suppression of displacement act to obscure the misalignment. Since our motion followed a linear path, we might imagine that continuity processes would "fill in" any gap of reduced visibility created by saccade, similar to the filling in seen for lines that stretch across the blind spot. However, our motion probe, when not corrected for the saccade-induced shift, was neither stable nor filled-in across the saccade. It had a significant, pre- to post-saccadic misalignment of about 10% to 20% of the saccade amplitude. The transition between the two segments was sometimes seen as a discrete break, and sometimes as a sharp curve, but the two segments were invariably seen as misaligned. In contrast, pre-existing spatial references appear to remove or attenuate the large but transient variations of the perceived location of brief probes (Jeffries, Kusunoki, Bisley, Cohen, & Goldberg, 2007; Van Wetter & Van Opstal, 2008).

Conclusion

Using a continuous motion probe, we captured and made directly visible a gross and continuing misalignment of perceived location that occurs around the time of the saccade. The perceived location of the trace was shifted at about the midpoint of the saccade. The shift carried the persisting trace of the pre-saccadic motion about 20% too far suggesting an over-compensation for the effects of the saccade.

Acknowledgments

We are grateful to current and former members of the Centre Attention and Vision (AV, BS, DJ, EH, FP, JAG, MR, SC, TBD, and TK) and especially to Rémy Allard for his comments and his help on the experimental method, and to Elodie Parison and Alice Szinte. This research was supported by a Chaire d'Excellence Grant to PC and a French Ministère de l'Enseignement Supérieur et de la Recherche Grant to MS.

Commercial relationships: none.
Corresponding author: Martin Szinte.
Email: martin.szinte@gmail.com.
Address: Université Paris Descartes - Sorbonne Paris Cité, Paris, France.

References

Awater, H., Burr, D., Lappe, M., Morrone, M. C., & Goldberg, M. E. (2005). Effect of saccadic adaptation on localization of visual targets. *Journal of Neurophysiology, 93*(6), 3605–3614.

Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychological Research, 32*(3), 185–218.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436.

Breitmeyer, B. G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. *Acta Psychologica, 52*(3), 175–196.

Bridgeman, B. (2007). Efference copy and its limitations. *Computers in Biology and Medicine, 37*(7), 924–929.

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during

saccadic eye movements. *Vision Research, 15*(6), 719–722.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences, 17*(2), 247–258.

Burr, D. C., Holt, J., Johnstone, J. R., & Ross, J. (1982). Selective depression of motion sensitivity during saccades. *Journal of Physiology, 333*, 1–15.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences, 14*(4), 147–153.

Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision, 9*(5):29, 1–9, http://www.journalofvision.org/content/9/5/29, doi:10.1167/9.5.29. [PubMed] [Article]

Cornelissen, F. W., Peter, E. M., & Palmer, J. (2002). The Eyelink toolbox: Eye tracking with MATLAB and the psychophysics toolbox. *Behavior Research Methods, Instruments, & Computers, 34*(4), 613–617.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research, 36*(7), 985–996.

Duhamel, J.-R., Colby, C. L. & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255*(5040), 90–92.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, 103*(18), 7192–7197.

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology, 64*(2), 489–508.

Hershberger, W. (1987). Saccadic eye movements and the perception of visual direction. *Attention, Perception, & Psychophysics, 41*(1), 35–44.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics, 45*(2), 162–174.

Honda, H. (2006). Achievement of transsaccadic visual stability using presaccadic and postsaccadic visual information. *Vision Research, 46*(20), 3483–3493.

Jeffries, S. M., Kusunoki, M., Bisley, J. W., Cohen, I. S., & Goldberg, M. E. (2007). Rhesus monkeys mislocalize saccade targets flashed for 100ms around the time of a saccade. *Vision Research, 47*(14), 1924–1934.

Jonides, J., Irwin, D. E., & Yantis, S. (1982, January 8). Integrating visual information from successive fixations. *Science, 215*(4529), 192–194.

Jonides, J., Irwin, D. E., & Yantis, S. (1983). Failure to integrate information from successive fixations. *Science, 222*(4620), 188.

Kusunoki, M., & Goldberg, M. E. (2003). The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *Journal of Neurophysiology, 89*(3), 1519–1527.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403*(6772), 892–895.

Mateeff, S., & Gourevich, A. (1983). Peripheral vision and perceived visual direction. *Biological Cybernetics, 49*(2), 111–118.

Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin, 81*(12), 899–917.

Matin, L., & Pearce, D. G. (1965, June 11). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. *Science, 148*(3676), 1485–1488.

Müsseler, J., van der Heijden, A. H. C., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perception & Psychophysics, 61*(8), 1646–1661.

Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Ross, J., Morrone, M. C., & Burr, D. C. (1997, April 10). Compression of visual space before saccade. *Nature, 386*, 598–601.

Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research, 35*(16), 2347–2357.

Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly; Delays and localization errors in the visual system. *Nature Reviews Neuroscience, 3*(3), 191.

Sogo, H., & Osaka, N. (2001). Perception of relation of stimuli locations successively flashed before saccade. *Vision Research, 41*(7), 935–942.

Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision, 11*(2):4, 1–20, http://www.journalofvision.org/content/11/2/4, doi:10.1167/11.2.4. [PubMed] [Article]

Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I.

Predictive visual responses. *Journal of Neurophysiology, 78*(3), 1373–1383.

Van Wetter, S. M. C. I., & Van Opstal, A. J. (2008). Experimental test of visuomotor updating models that explain perisaccadic mislocalization. *Journal of Vision, 8*(14):8, 1–22, http://www.journalofvision.org/content/8/14/8, doi:10.1167/8.14.8. [PubMed] [Article]

von Helmholtz, H. (1867). *Handbuch der physiologischen Optik*. Leipzig: Leopold Voss.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften, 37*, 464–476.

Watanabe, J., Noritake, A., Maeda, T., Tachi, S., & Nishida, S. (2005). Perisaccadic perception of continuous flickers. *Vision Research, 45*(4), 413–430.

Wichmann, F. A., & Hill, N. J. (2001a). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*(8), 1293–1313.

Wichmann, F. A., & Hill, N. J. (2001b). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception & Psychophysics, 63*(8), 1314–1329.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research, 48*(20), 2070–2089.

4.3 Compensation for head movements

4.3.1. Objectives and summary of results

In the third study of this thesis, we adapted the procedure of the first study (Szinte & Cavanagh, 2011) to evaluate whether the correction of location occurs not only for eye movements but also head movements. Several studies have evaluated the ability to keep track of a target's position in the world despite movements of the head. Specifically, the compensation for both active and passive head and body roll is quite accurate (Bloomberg et al., 1991; Klier et al., 2005, 2006; Medendorp et al., 2002; Van Pelt, Van Gisbergen, & Medendorp, 2005) as is that for head and body translation (Berthoz et al., 1995; Israël & Berthoz, 1989; Klier et al., 2008; Li & Angelaki, 2005; Medendorp, Tweed, et al., 2003; Wei et al., 2006). In these studies, a target was flashed just before a head movement and observers then reported its remembered location by saccading or pointing to it. In contrast, our procedure involved a direct perceptual evaluation of the displacement by presenting two targets, one before and the other after the observers' head movement. We use two types of active head movements: head roll and fore-aft translation. With this procedure, we determined the degree of compensation of the first probe by analysing its apparent displacement to the second location. If its displacement was seen in spatial coordinates, then the compensation was accurate.

The results show that the displacement between the first and second probe is seen mostly in spatial rather than retinal coordinates. Nevertheless, observers reported systematic biases in the orientation of the displacements, tilted by about 14° away from vertical in the head roll condition and by about 4° away from horizontal in the head translation condition. These biases corresponded to a significant under-correction of about 20% of the required amount for head roll and to a smaller but non-significant over-correction of about 10% of the required amount for head fore-aft translation.

This disparity with previous literature may reflect the difference of time allocated to compensate for the head movement. The earlier reports of accurate compensation for head movement used memory-based tests that allowed a delay of up to two seconds before the location report was made. In our case, the head movement was just ending when the second probe appeared on the screen.

The longer delay prior to the report in the previous studies might have allowed the visual system to combine other signals that are available after the head movement (retinal input, proprioception or vestibular information of the head position) with the predictive signals (efference copy) available before and during the head movement. In our case observers' judgment would have to rely more on the predictive signals since accurate feedback signals are not expected to be fully available during the head movement.

Contrary to previous reports of accurate, almost perfect, compensation for head movements, we observed systematic errors for head roll but not for head translation. We explain these results by the fact that in our procedure the slow feedback signals were not fully available. Inaccurate compensation

might then reflect the slower integration of vestibular information for head roll compared to head translation. Whatever the source of the error, whether it is the incoming signals indicating the extent of the head movement (optic flow, efference copy, proprioception, or vestibular input) or the conversion of these head movement signals into a predicted displacement (remapping) of target location on the position map (the saccade maps), it must be larger (under-correction) for head roll than for head translation.

Visual space constancy across head roll and head translation

Article submitted to Journal of Neurophysiology

Martin Szinte[1,2], Stéphanie Correia [1,2] and Patrick Cavanagh[1,2]

Affiliations

1. Laboratoire Psychologie de la Perception,
   Université Paris Descartes, Sorbonne Paris Cité, Paris, France.
2. CNRS, UMR 8158, Paris, France.

Abstract

Stationary objects are displaced on the retina whenever the eyes or head move but the visual system attempts to correct for the effects of self-motion to recover object's location in the world. To measure the accuracy of the compensation, we adapted a procedure previously used for saccades (Szinte and Cavanagh, 2011) in which two target dots are presented sequentially, one before and one after a head roll or a fore-aft head translation. Human observers made head rolls of approximately 60° around the visual axis or fore-aft translations of the head, traveling about 20 cm toward or away from the screen. The dots' spatial displacement was vertical for head roll and horizontal for head translation. Retinal displacement was then oriented about 75° away from vertical for head roll and 45° away from horizontal for head translation. In both cases, observers reported seeing an oblique component in the perceived displacement with significant errors of compensation for head roll (error of 20% of the head movement amplitude), but the errors for head translation (10%) did not reach significance. Head roll results differ from previous studies that had shown accurate compensation. These studies were all based on delayed reports of memorized location whereas here we used a perceptual judgment made near the end of the head movement. This difference suggests that the accurate correction of location for the effects of head movement takes time and with extra time, possibly calls on additional signals.

Keywords

Head movement, space constancy, remapping, active roll, active translation.

Introduction

We mainly rely on our vision to navigate in our environment but whenever we move our eyes, head or body to explore our environment, the image on our retina changes dramatically. Nevertheless we perceive a reassuringly stable world with which we easily and correctly interact. This visual space constancy is thought to rely on an updating of the retinal projection to correct for the effect of self-motion and predict what the world will look like after the movement. These updating processes have been studied physiologically for saccades (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990) and similar processes might also be used to compensate for head movements (Medendorp, Smith, Tweed, & Crawford, 2002). There are several visual and extra-visual cues that can be used to predict the effects of head movements such as a copy of the motor command send to the muscles (called corrolary disharge or efference copy, Sperry, 1950; von Holst & Mittelstaedt, 1950), feedback signals of the vestibulo-ocular reflexes (Klier, Angelaki, & Hess, 2005; Klier, Hess, & Angelaki, 2008), body or head proprioception (Blouin, Gauthier, van Donkelaar, & Vercher, 1995; Israël & Berthoz, 1989; Mergner, Nasios, & Anastasopoulos, 1998), vestibular information about head position (see review, Angelaki & Cullen, 2008; Cullen, 2012) and retinal input signals (Gibson, 1950, 1966; O'Regan, 1992).

Interestingly, several studies have investigated the quality of the compensation made for different head movements. These studies reported accurate correction in humans and monkeys for active and passive head and body roll (Bloomberg, Jones, & Segal, 1991; Klier et al., 2005; Klier, Hess, & Angelaki, 2006; Medendorp et al., 2002; Van Pelt, Van Gisbergen, & Medendorp, 2005) as well as active and passive forward-backward head or body translation (Berthoz, Israël, Georges-Francois, Grasso, & Tsuzuku, 1995; Israël & Berthoz, 1989; Klier et al., 2008; Li & Angelaki, 2005; Medendorp, Tweed, & Crawford, 2003; Wei, Li, Newlands, Dickman, & Angelaki, 2006). These authors evaluated the accuracy of a delayed action (saccade or pointing) made to the location of an object briefly presented before the head movement. Under these conditions, subsequent movements were then correctly directed to the flash's position in space rather than to the location corresponding to flash's position on the retina.

Here, we adapted a procedure used initially for eye movements (Szinte & Cavanagh, 2011) to evaluate the accuracy of processes that correct for head movements. Two dots were displayed; one before and one after the observers' head movement and observers reported the perceived angle between dots. In contrast with previous studies that used a memory based movement task, our procedure involve a direct perceptual evaluation of the displacement angle of the dots occurring as soon as the second one appeared.

Using this procedure, we evaluated the accuracy of correction for head movements in two experiments in which observers judged the displacement angle seen between the dots when an active head roll or an active head fore-aft translation was inserted between the dots presentations. These two types of head movements were chosen because they modify the angle of the motion on the retina and because feedback information about the head movements can be acquired from two organs of

the vestibular system, the semi-circular canals for head roll and the otoliths for head translation.

In contrast with previous reports of accurate updating for active and passive head roll, we observed systematic biases in the displacement angle between our two probes for this first type of head movement. On the other hand, although observers saw some slant in the dot displacement across fore-aft translation, the compensation was fairly accurate for this second type of head movement.

Materials and methods

Observers

Six observers (2 authors and 4 naive to the purpose of the experiment, age 22-30 years, 1 female, 5 males) took part in the experiments. All had normal or corrected to normal vision, and no known neuromuscular or neurological deficit. The experiment was carried out according to ethical standards specified in the Declaration of Helsinki and was approved by the Ethics Committee from the Université Paris Descartes. All observers gave written informed consent before participating in the experiment.

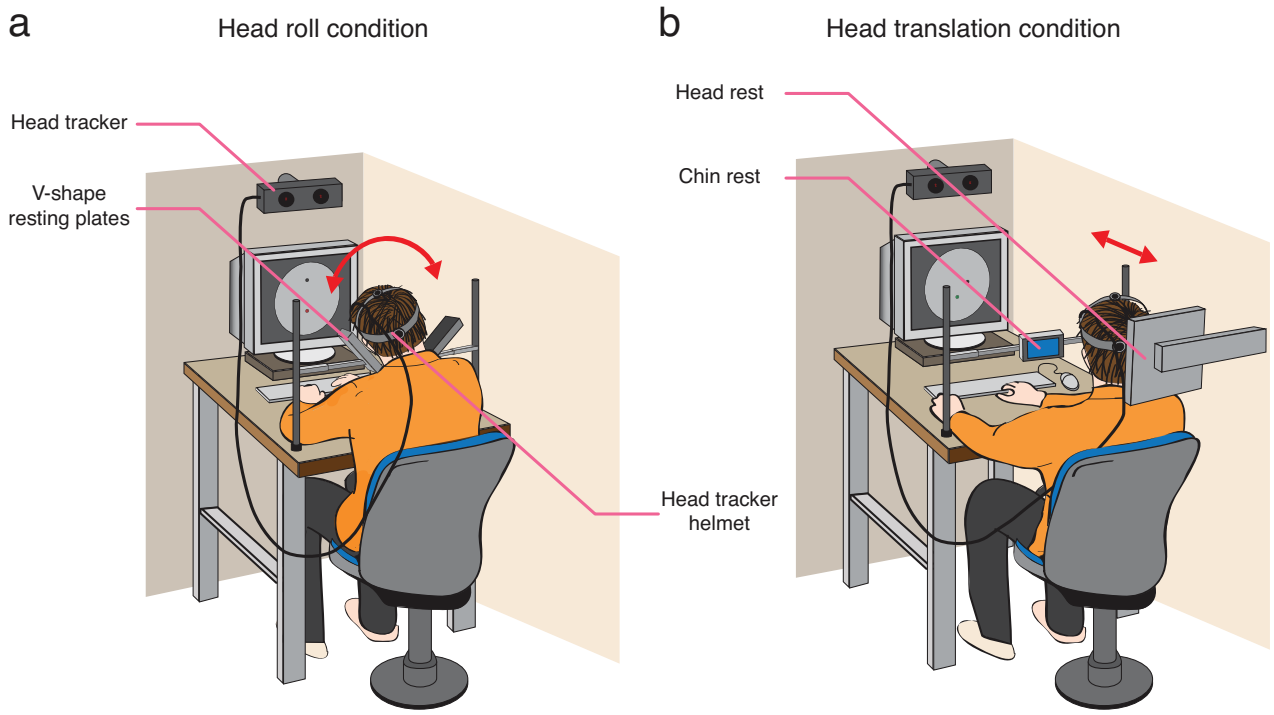


Figure 1. Experimental apparatus. Observers faced a CRT screen covered by a circular mask positioned at 60 cm from metal restraints designed for the head roll and the head translation conditions. They wore a head-tracking helmet while the head-tracking scanner was positioned above the screen. (a) For the head roll condition, V-shaped resting plates were positioned in order to constraint the head rolls to a maximum tilt of 40 degrees to the left and to the right. (b) For the head translation condition, a forward pad was positioned at the level of the observers' chin together with a back pad at the level of the back of observers' head. These buffers constrained the head fore-aft translations to more or less 20 cm.

Apparatus

Observers were seated in a silent and dimly lit room, in front of a gamma-linearized 22" Compaq P1220 CRT display screen (Compaq, Houston, TX, USA) with a spatial resolution of 1024 by 768 pixels and a vertical refresh rate of 100 Hz. The experiment was controlled by an Apple iMac Dual Intel-Core Xeon computer (Apple inc., Cupertino, CA, USA). Manual responses were acquired via a standard keyboard. The experimental software employed for the elaboration of the stimulus display and response collection was implemented under Matlab (Mathworks, Natick, MA, USA) using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997). Three-dimensional head orientations as well as three-dimensional head spatial locations were recorded using an optical motion tracker (LaserBird, Ascension, Burlington, VT, USA). This head tracker is composed of a lightweight sensor worn on a helmet held fixed to the front of the head and of a fan-shaped laser beam scanner positioned above the screen (see Figure 1). Head coordinates monitoring was implemented with an in-house toolbox using Matlab. We built metal restraints for the head roll and head translation conditions. For the head roll condition, V-shaped resting plates were positioned in order to restrict the head roll to a maximum of 40 degrees tilt to the left and to the right (see Figure 1a). For the head fore-aft translation condition, a forward pad was positioned on the table at the level of the observers' chin, and a back pad was positioned 40 cm away from the forward pad at the level of observers' head (see Figure 1b). Taking into account a mean head profile width of 20 cm, the fore-aft head translation for each trial was about 20 cm. Both head roll and head translation rests were positioned so that the observers saw the screen at a distance of 60 cm (or 80 cm when they move their head backward), with the eyes at the same height as the fixation target.

Stimuli

Stimuli were displayed on a circular screen (a screen to which we applied a circular mask), on a grey background (46.4 cd/m). The 0.5° diameter fixation bulls-eye target, displayed 5° below the screen center, alternated between red (20 cd/m²) and green (20 cd/m²) for the purpose of synchronizing the head movements. In addition there were two circular, 0.5° diameter black probes (0.5 cd/m²) placed 5° above the screen center and separated by 3° from each other.

Procedure

Each observer was ran in two conditions in which they were instructed to perform either head roll or head fore-aft translations. At the beginning of each trial, the screen displayed a fixation bulls-eye target, which was either red or green. Observers fixate the colored target during the whole trial, and its initial color instructed whether they should, in the *head roll condition*, tilt their heads to touch either the left or right resting plate or in the *head translation condition*, move their heads either forward or backward to touch the front or the back pad. We monitored online the head position and trials began only when observers maintained their head at the correct location for 600 msec.

Each trial was composed of two red-to-green alternations of the fixation target made every 1.2 sec. While the first alternation reminded observers about the rhythm of the fixation target color changes, observers were instructed to only move their heads in synchrony with the second alternation. During this second alternation, two black dots (probes) were presented sequentially, one before and

one after the fixation target color changes. Each probe was presented for 600 ms and separated by an interval of 600 ms between each other. At the end of each trial, observers reported whether they perceived the displacement between probes as tilted clockwise or counter-clockwise relative to the vertical.

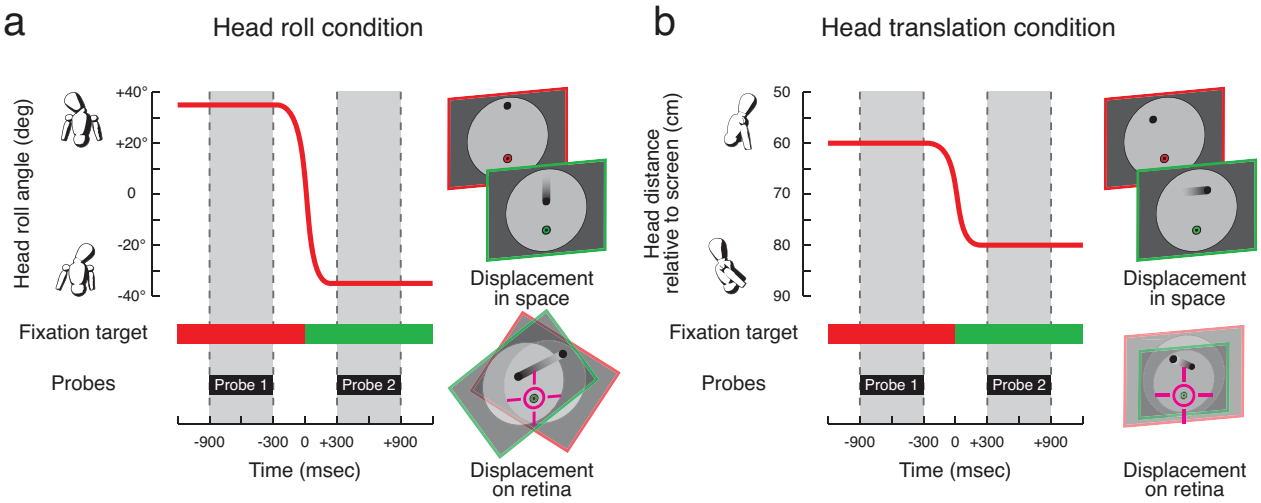


Figure 2. Experimental procedure. Each panel plots theoretical observer's head position as a function of time as well as the color of the fixation target (horizontal red and green rectangles) and of presentation of the probes (vertical gray areas and black rectangles). The right side of each panel depicts the probe displacement before (red frames rectangles) and after (green frames rectangles) the head movement, in space (top) or on retina (bottom). (a) For the head roll condition, observers executed either rightward (as described in this figure) or leftward head roll movements. Two probes were presented sequentially and observers attempted to perform the head rolls between the two presentations. The probes could either be displaced downward (as presented here) or upward on the screen. The head roll occurring between probe presentations causes the probes' displacement to be tilted on the retina even though they were aligned vertically in space. (b) For the head translation condition, observers moved either backward (as presented here) or forward. Two probes were presented sequentially and observers attempted to perform the head translation between the two presentations. The probes could either be displaced rightward (as presented here) or leftward on the screen. The head translation occurring between probe presentations causes a tilted displacement on the retina even though the two probes were aligned horizontally in space. For both head movement conditions, the two probes were displaced with different angles around the vertical or horizontal axis and observers were asked on each trial to report the direction of the displacement perceived (either clockwise or counter-clockwise).

Head roll condition. Head movement across probes presentations could equiprobably be rightward (from about +30° to -30° from the head vertical) or leftward head roll (from about -30° to +30°) from one resting plate to the other. Observers were instructed to roll their head around an axis centered on the fixation target and to minimize yaw and pitch rotations of the head as well as any lateral head translations. On each trial, the probes angles were selected equiprobably from one of nine possible angles centered on a vertical axis, -60°, -45°, -30°, -15°, 0°, +15°, +30°, +45° and +60°, with 0° corresponding to the vertical displacement, negative values to right-tilted displacements (clockwise) and positive values to left-tilted displacements (counter-clockwise). Finally probes could equiprobably be presented top-first or bottom-first, giving respectively downward and upward probes displacement trials.

Head translation condition. Head movements across probes presentations could equiprobably be forward (about 80 cm to 60 cm from the screen) or backward head translation (60 cm to about 80 cm from the screen) from the chin to the back head pad. Observers were instructed to move their head

in the direction of an axis centered on the fixation target and minimize lateral head translations as well as head roll, yaw or pitch rotations. On each trial, the probes angles were selected equiprobably from one of nine possible angles centered on an horizontal axis, -60°, -45°, -30°, -15°, 0°, +15°, +30°, +45° and +60°, with 0° corresponding to the horizontal displacement, negative values to left-tilted displacements (counter-clockwise) and positive values to right-tilted displacements (clockwise). Finally, probes could equiprobably be presented right-first or left-first, giving respectively leftward and rightward probes displacement trials.

For each head movement condition (roll or translation), the combination of all conditions gave a set of 36 trials (head movement directions x probe motion angles x motion directions). This set was repeated 15 times, leading to 540 trials per condition of head movement. Each observer executed 24 experimental blocks (12 in head roll, 12 in head translation condition) composed of 45 trials each and lasting each about 7 min. Blocks within each head movement condition (roll or translation) were grouped by six and randomly interleaved in different order for different observers.

Data analyses

Head movements data were analyzed offline using an adaptation of Engbert & Mergenthaler (2006) eye movement detection algorithm, based on one-dimensional head velocity, computed from subsequent samples in the head position series (either roll angle or head distance from screen). The thresholds for peak velocity and minimum duration for head movement detection were 3 SD and 50 ms. The percentages of “right” responses were plotted as a function of the presented angle to obtain a psychometric function and a point of subjective equality (corresponding to a point of subjective verticality for head roll and to a point of subjective horizontality for head translation condition), and the bias (inverse of the point of subjective equality). Psychometric functions were fitted with Palamedes toolbox (http://www.palamedestoolbox.org).

Results

We measured observers’ biases of seeing vertical or horizontal displacement as tilted when presented respectively across head rolls or head fore-aft translations. These biases could be evaluated by taking the inverse of the angle necessary between probes to perceive displacement as being vertical across a head roll or horizontal across a head translation. To do so, we first selected trials where head movements occurred in between probes presentations, rejecting trials in which head movements ended before the offset of the first probe or started after the onset of the second probe. Such selection insures that at least a portion of the head movement occurred in between probes presentations and that the two probes couldn’t have been seen from the same initial or final head position. Overall, for the head roll condition 3240 trials were run across all observers, our offline analyses led us to reject 759 trials, leaving 76.6% correct trials (across observers, the proportion of correct trials varied from 61.5% to 97.4%). For the head translation condition 3240 trials were run across all observers, offline analyses led us to reject 693 trials, leaving 78.6% correct trials (from 60.0% to 95.4% across observers).

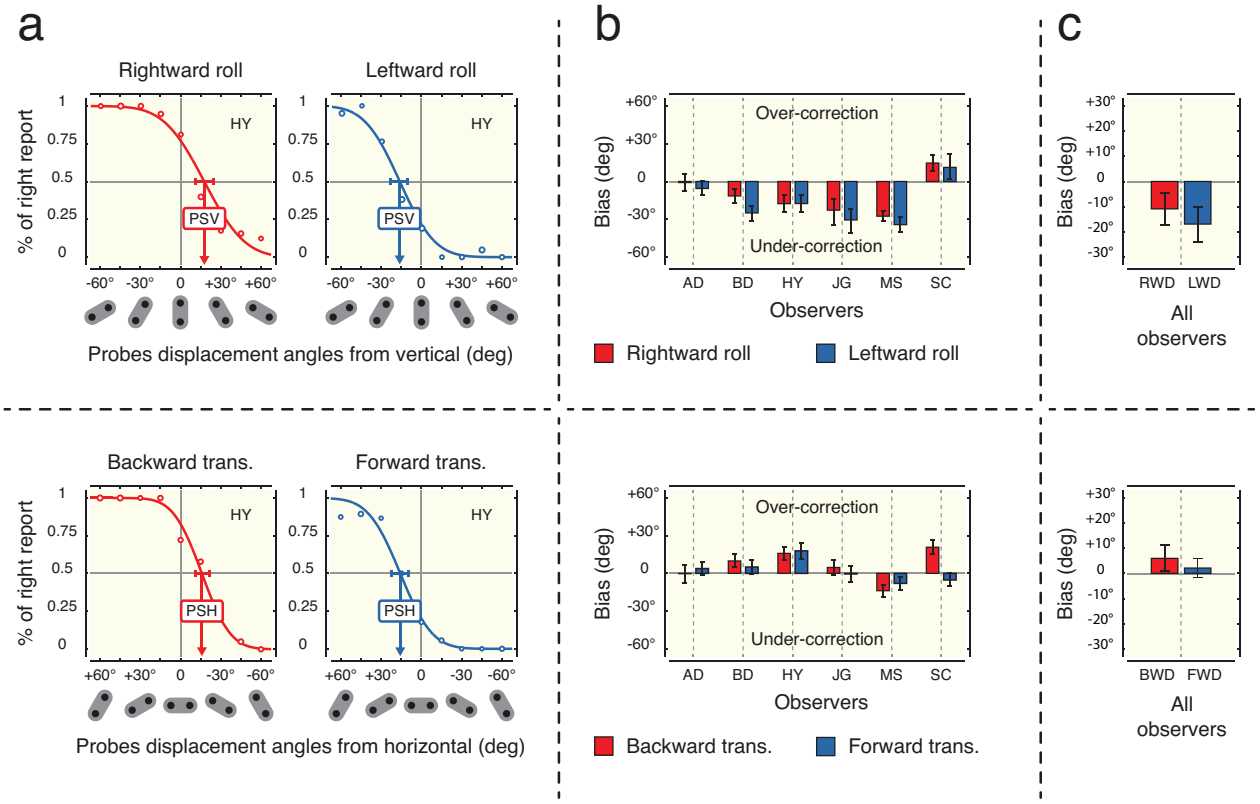


Figure 3. Individual and group result in the head roll and head translation conditions. (a) Proportion of "right" report in function of the probes displacement angles from vertical/horizontal, for one observer ('HY') for rightward/forward (red curves) and leftward/backward (blue curves) of selected trials from the head roll (top panels) and the head translation condition (bottom panels). Psychometric functions were fitted to estimate the point of subjective verticality (PSV) or horizontality (PSH), i.e., the probes displacement angle from vertical/horizontal leading to the equal perception of "right" or "left" report. (b) Bias results for all observers and for the group. Bars represent the evaluated bias for each observers and head movement directions individually. Error bars for each observer indicate 95% confidence interval computed by bootstrapping (iterations = 1000). (c) Average biases across observers. Bars represent average values of biases across observers (n=6) for the two directions of head movements in both head roll and head translation condition, note that the bias axis is multiply by two when compared with the axis in panel b. Error bars show the SEM across observers.

We plotted psychometric functions based on the reports from these selected trials to determine observers' biases for the four combinations of two head movement directions (rightward/leftward in head roll condition or backward/forward in head translation condition) and the two probe displacement directions (downward/upward or rightward/leftward). From these functions we determined observers' biases by taking the inverse of the angles at which the "right" report reached 50%, level defined as the point of subjective verticality (PSV) for the head roll condition and as the point of subjective horizontality (PSH) for the head translation condition. At this level, in order to perceive the displacement as it is in space, the first probe location should be compensated for the amplitude of the executed head movement, in its opposite direction. If the compensation matched the executed head movement, there should be no bias (PSV and PSH at 0°). However, head compensation could be incorrect and could arise with either an under or and over-correction, leading to the perception of tilted probe displacement. We collapsed the two directions of displacement, correcting for the inversions of probe angle and direction report. Figure 3a shows the psychometric curves for one observer obtained for the two directions of head movement in both head roll and head translation conditions. The opposite directions of head movements will reverse the direction of reported bias, if any.

For example, in Figure 3a the fitted curves for the head roll condition indicate PSV of +17.6° (CI: [+10.9°, +23.8°]) and -16.6° (CI: [-23.2°, -10.8°]) for rightward and leftward trials, respectively, where both biases represent an under-correction of the head movement. For head translation condition, the fitted curves indicate PSH of -15.9° (CI: [-21.3°, -10.8°]) and +15.7° (CI: [10.2°, 21.6°]) for forward and backward trials, respectively, indicating an over-correction of the head movement again in both head direction cases. We then combined the biases for the two head directions and Figure 3b summarizes these combined results for all observers by presenting their biases for both head roll and head translation conditions.

As shown in Figure 3b, observers mostly under-corrected the head roll movement (5 observers out of 6) and over-corrected the head translation movements (4 observers out of 6). Figure 3c summarizes the biases observed by showing the average value for the group. Between observers, we see here an under-correction for head roll of -13.9° ± 7.1° (-10.9° ± 7.0° for rightward, -17.0° ± 7.7° for leftward head roll) and a smaller over-correction for head fore-aft translation of +4.2° ± 4.7° (+6.2° ± 5.5° for backward, 2.2° ± 4.1° for forward head translation).

However, these results do not yet tell us about the accuracy of head compensation in terms of percent of required correction. The actual correction that would produce veridical perception depends on the amplitude of the head movement as well as their consequences on the projections of the probes locations on the retina. We therefore computed, for each type of head movement, the amount of compensation as a proportion of the correction for accurate perception.

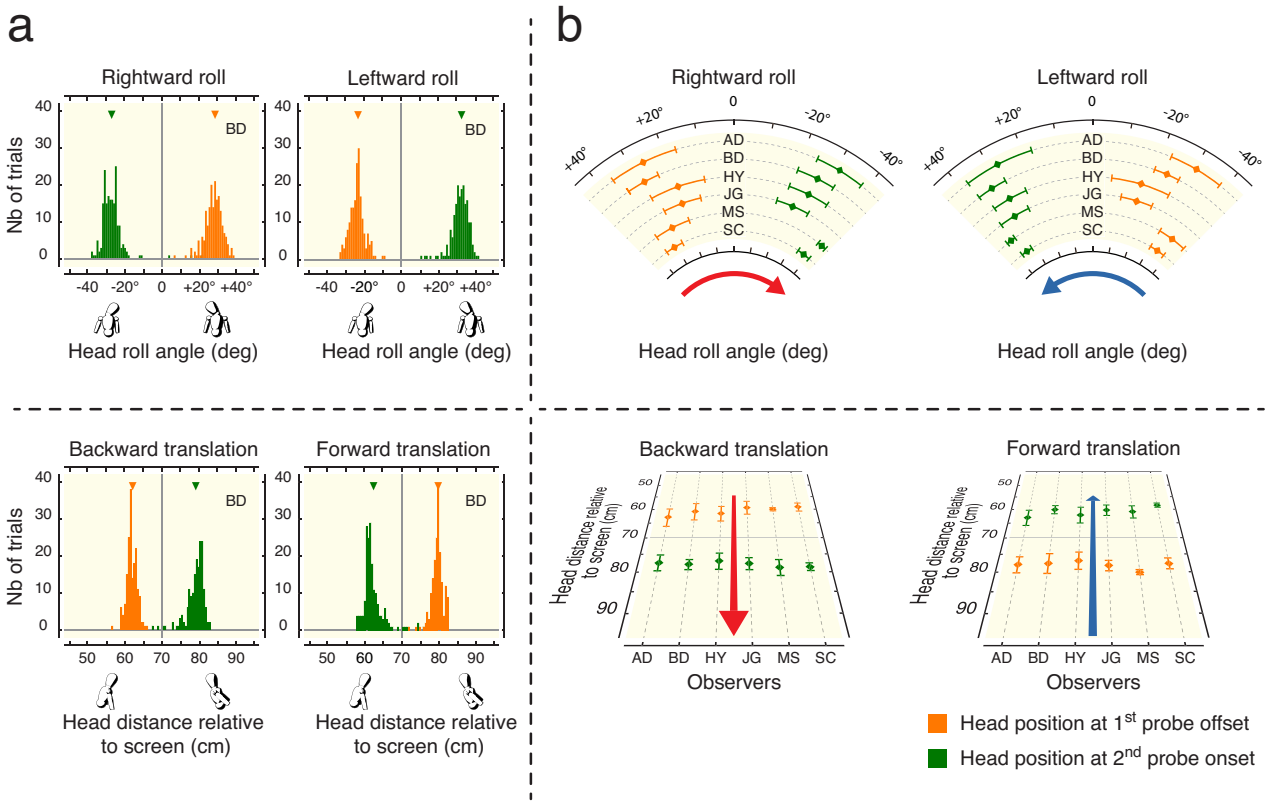


Figure 4. Head movements. (a) Distributions of head position for one observer ('BD') at the moment of first probe offset (in orange) and at the moment of the second probe onset (in green) for head roll (top panels) and head translation (bottom panels) conditions. Arrowheads at the top of each figure show the mean position of the head. (b) Means head position at the 1st probe offset and of the 2nd probe onset across all observers (n=6) for the head roll (top panels) and head translation (bottom panels) conditions. Error bars show the standard deviations of the head positions across trials.

To do this, we first determined the distribution of head position at the offset of the first probe and at the onset of the second probe. These two head positions determined on each trial the actual head movement amplitude that has to be compensated. Figure 4a shows these distributions for one observer and Figure 4b show the mean head positions for the group. Using these mean head positions, we computed the average angle on the retina between the offset of the first and onset of the second probes.

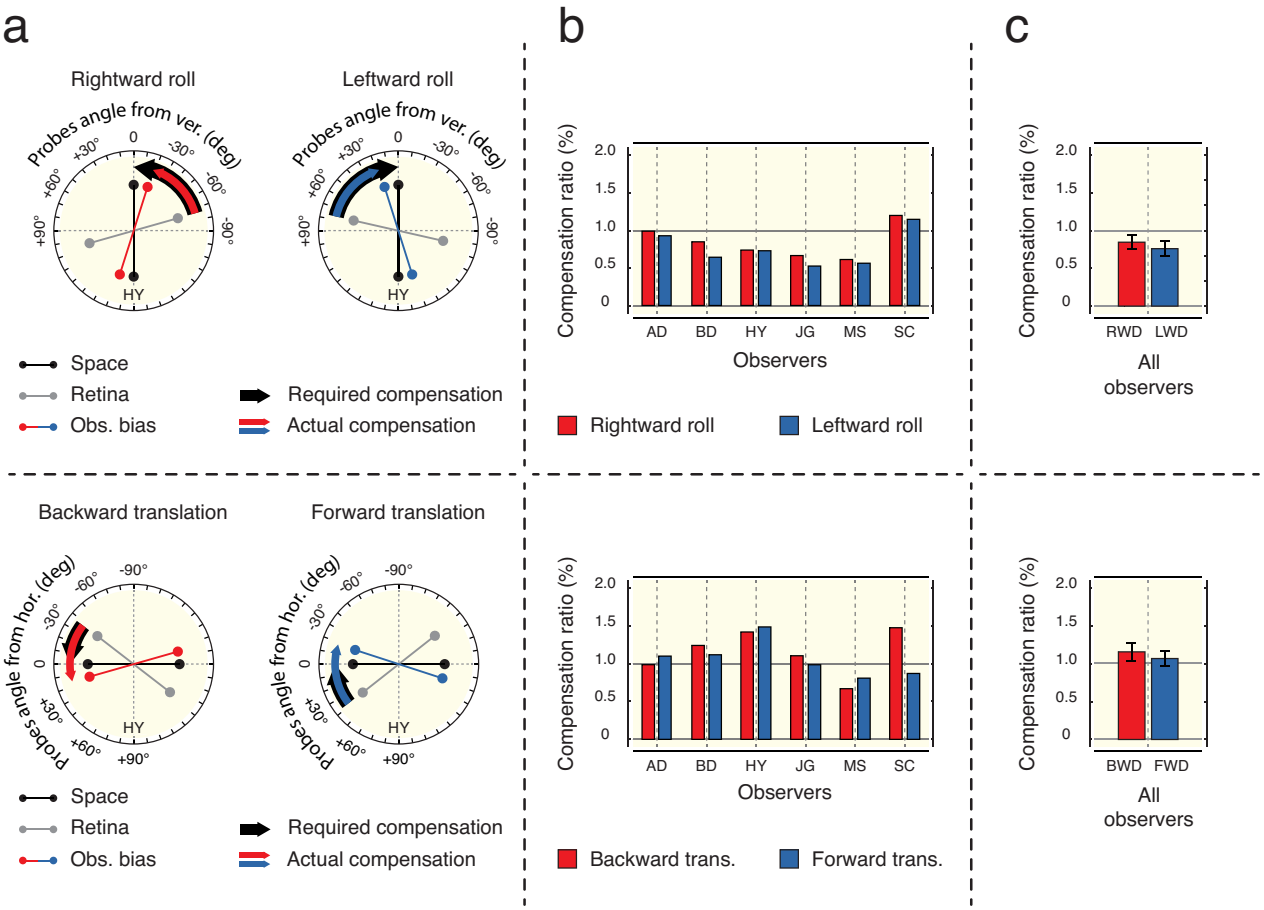


Figure 5. Head movement compensations. (a) Probes displacement angles of one observer ('HY') from vertical/horizontal for rightward/leftward head roll condition and backward/forward head translation condition. Circular figures display the probes angle in space (black dots), on the retina (gray dots) and the observed bias (red dots). We determined for each condition the required compensation (black arrows), that is the angle going from the retinal to the spatial displacement of the probes as well as the actual compensation (red and blue arrows), that is the angle going from retinal displacement to the evaluated bias. (b) Compensation ratio of observers individually. Bars represent the ratio between the actual compensation and the full compensation determined individually for each observer, head movement directions and conditions. (c) Average of compensation ratio across observers (n=6). Error bars show the SEM across all observers.

With these retinal angles we then determined the ratio of the actual to the required compensations for each observer individually. Figure 5a shows for one observer the retinal and the spatial angle of the probe displacement as well as the bias observed for the two directions of the head roll and head translation conditions. The figure also illustrates the actual and the required compensations for all combinations of head movement conditions and directions. Figure 5b show head movement compensation ratios for each observer individually. Notice that a ratio of 0 denotes an absence of head movement compensation and thus a report of the retinal displacement, while a ratio of 1 represents a total compensation with an accurate report of the probes displacement in space. As

shown in Figure 5c, across observers we found compensation ratios of 80% ± 10% for the head roll (84% ± 10% for rightward and 75% ± 11% for leftward head roll) and of 111% ± 10% for the head translation (115% ± 13% for backward, 107% ± 10% for forward head translation). An ANOVA with head movement condition as variable show a significant difference between head roll and head translation condition ($F[1,5] = 7.90$, $p < 0.05$). Moreover, subsequent planned comparisons between the observed compensation ratios and a ratio of 1 (accurate compensation level) show that head rolls were significantly under-estimated ($t[5] = -2.65$, $p < 0.05$), whereas there was no significant difference from accurate compensation for the head translation condition ($t[5] = 1.36$, $p = 0.15$).

Finally, we used the head tracking data to select trials where the major portion of the head movement was executed between the offset of the first probe and the onset of the second (trials where head positions at the offset of the first probe and onset of the second fall inside 1SD of the mean head positions at these two moments). This eliminated trials where most the head movement was executed either before the offset of the first probe (early head movements) or after the onset of the second probe (late head movements), conditions which would have allowed both probes to have been seen from very similar head positions. For the head roll condition, a further 966 of the 2481 trials failed to meet this criterion, leaving 61.1% of the correct trials (not rejected for other reasons, see above) and 46.8% of all head roll trials (across observers, the proportion of selected trials ranged from 52.1% to 79.3% of correct trials and 32.0% to 75.0% of all trials). For the head translation condition, a further 772 trials from the 2547 correct trials were rejected, leaving 69.7% of the correct trials and 54.8% of all head roll trials (across observers, from 61.8% to 76.1% of correct trials and 41.1% to 68.7% of all trials).

We reanalyzed these remaining trials as before and found an average bias of -15.6° ± 9.0° in head roll (against -13.9° ± 7.1° before trials selection) and +4.3° ± 4.6° in head translation condition (against 4.2° ± 4.7° before). Using the proportion of correction analysis as described before, we found significantly different compensation ratios between two head movement types ($F[1,5] = 10.31$, $p < 0.05$). The proportion of correction was 78% ± 11% for the head roll (against 80% ± 10% before) and 111% ± 10% for the head translation condition (against 111% ± 10% before).

Again subsequent planned comparison of the observed compensation ratios with the ratio of 1 show that compensation for head roll was significantly under-estimated ($t[5] = -2.67$, $p < 0.05$) but the observed overestimation of head translation was not significant ($t[5] = 1.48$, $p = 0.13$).

This last analysis, screening out trials where both probes may have been seen from almost one head position, showed results very similar to the unscreened analysis. This suggests that the error of correction effects rely mostly on trials where the head movement occurred in between probes presentation and less on early and late head movement trials where the errors would have been smaller.

Discussion

Here we presented two probes in succession, one mainly before and one mainly after the execution of an active head roll or an active head fore-aft translation. The results show that the displacement between the first and second probe is seen mostly in spatial rather than retinal coordinates. Nevertheless, observers reported systematic biases in the orientation of the displacements, tilted by about 14° away from vertical in the head roll condition and by about 4° away from horizontal in the head translation condition. These biases corresponded to a significant under-correction of about 20% of the required amount for head roll and to a smaller but non-significant over-correction of about 10% of the required amount for head fore-aft translation. These results challenge previous reports of accurate updating for active and passive head roll (Bloomberg et al., 1991; Klier et al., 2005, 2006; Li & Angelaki, 2005; Medendorp et al., 2002; Van Pelt et al., 2005) but confirm, using a novel procedure, the reports of accurate updating for active head translation (Berthoz et al., 1995, 1995; Klier et al., 2008; Li & Angelaki, 2005; Medendorp et al., 2003; Wei et al., 2006).

The disparity in results observed between previous reports and ours could certainly be explained by the differences in methods. The main difference is that previous studies used a memory-based judgment procedure in which observers performed a delayed action to the remembered location of a target that had been briefly flashed (100 ms to 200 ms duration) before executing the head movement. The delay between the presentation of the target to-be-localized and the go signal to make the pointing or saccade response varied from 1.5 second for passive movements (Klier et al., 2005, 2006, 2008; Li & Angelaki, 2005) to 2 seconds for active head roll and translation (Medendorp et al., 2002, 2003). During these two seconds several signals may contribute to the recovery of the pre-movement location that might not be available in our more rapid procedure. Indeed while we left 600 ms between the first and second probe, the head movements on average lasted 725 ms (706 ms for head roll and 744 ms for head translation), starting 53 ms before the first probe offset (70 ms for head roll and 36 ms for head translation) and ending 47 ms after the second probe onset (11 ms for head roll and 82 ms for head translation). In the majority of the trials used for our analysis, the head movement was just ending when the second probe appeared on the screen.

However, this difference in delay for the two judgment procedures holds for both of our head movement conditions but we found a significant breakdown of location correction only for head roll and not for head translation. To find an explanation for this difference, we next examine the different signals available to the visual system to correct the change in retinal projections due to the head movement.

One signal available in our experiment that was not available in previous studies was optic flow from experimental room during the head movement. Our experiments were performed in dim light so that the observers saw the edge of the monitor as well as the testing room in their peripheral vision. In the previous studies (Berthoz et al., 1995; Bloomberg et al., 1991; Israël & Berthoz, 1989; Klier et al., 2005, 2006, 2008; Li & Angelaki, 2005; Medendorp et al., 2002, 2003; Van Pelt et al., 2005; Wei et al., 2006), the head movements were made in total darkness, except for the small fixation dot

to stabilize the eyes during the head movement. These motion cues from the periphery have been shown to be influence corrections for active head translation, at least when a delay between the head movement and the response was available (Medendorp et al., 2003). Although these optic flow cues might contribute to more accurate correction for the head movement, we have no evidence that they would do so to a different extent for head roll versus head translation.

Proprioception is a second important signal in our experiment that indeed differs between our two conditions. In particular head roll involves neck muscles whereas fore-aft translation involves the torso. Proprioceptive cues to head motion would be available only during the head movement and even then with some transmission and processing delay. If proprioceptive signals for the torso were available before those for the neck, it might explain why the roll movements were less well corrected. If both then became available at longer delays, it would also explain why the previous articles found accurate correction for both types of head movements. However, there is no evidence for a longer delay for the neck muscles, and if anything, because of shorter transmission distances, we would expect the opposite.

A third set of signals from vestibular organs contributes an estimate the direction and amplitude of head roll and fore-aft movements.

We specifically choose our head movements because each principally activates a different organ of the vestibular system. The semi-circular canals respond strongly for the rotations of the head roll movement whereas the otoliths respond most strongly to the linear acceleration of the fore-aft head translation (Angelaki & Cullen, 2008; Cullen, 2012). We speculate then that the signals from the semi-circular canals for head roll might be more slowly integrated than the signals from the otoliths leading to an early under-compensation for head roll that would nevertheless become more accurate with a delayed judgment.

However, our two head movement conditions did not isolate pure roll or pure fore-aft translation. The head roll was accompanied by systematic head yaw rotations (less than 10°) and the translation movement was accompanied by systematic elevations in the head height relative to the fixation target (less than 5 cm). These intrusions of other types of head movement might have played a role in the errors we observed, but they cannot explain the difference between our results and previous active head movement studies which most likely had similar intrusions (Medendorp et al., 2002, 2003).

Counter-roll of the eyes (cyclotorsion) might also have been a factor during our head roll condition. We did not measure the amplitude of the cyclotorsion response but previous reports describe counter-roll of less than 5° for head roll of 30° (Haslwanter, Straumann, Hess, & Henn, 1992). In our case the head was tilted 60° and the counter-roll would act to reduce the size of the retinal displacement of the probes. With less retinal shift to counteract than the physical roll would specify, our measured errors may, if anything, underestimate the proportional error in correction.

Finally, the last signal available in our case is the efference copy of the motor signal for the head movement (Sperry, 1950; von Holst & Mittelstaedt, 1950). Klier and Angelaki (2008) have suggested that efference copy plays little or no role in head movement compensation because they no difference

were found in correction of location between active (where efference copy is available) and passive (where it is not) head movements. However since we do not find the same accuracy as the authors, it is possible that efference copy does play a role in our more perceptual location judgments. If this were the case, we would have to propose that the efference copy for head roll is less accurate than for fore-aft translation. We are not aware of any evidence that supports this difference.

So across the various signals that might contribute to a correction of location for the head movement, we see no obvious explanation for the difference we find between head roll and translation. The different vestibular organs engaged by these two head movements may play a role but there is no evidence yet that this is the case.

What is the process that uses some combination of these signals to effect the actual correction? We favor the same process that has been proposed to correct for the effects of eye movements on target locations: remapping (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Duhamel et al., 1992; Wurtz, 2008). This proposal assumes that the location of target-related activity codes the position of attended targets on the saccade maps even when no saccade is made to that target. When an eye movement is made, efference copy is used to shift the target-related activity to the location that the target will have after the saccade. We assume a different set of signals predicts where the target will be after a head movement and remaps the target-related activity to compensate for the target change in retinal coordinates. In our experiments here, that target is no longer present after the head movement, but a second probe is and the persistent activity representing where the first target was expected then permits a judgment of the displacement between the first and second probe.

We however admit that this hypothesis is purely speculative since we cannot rule out the use of the other signals or of other mechanism for space constancy. Subsequent studies in which the different signals will be carefully controlled are then necessary to draw a more accurate picture of the compensation for head movement, and especially to understand the loss of accuracy for head roll.

Conclusion

Using a probe displacement test, we demonstrate that displacements across two types of head movements are seen more in spatial than retinal coordinates. Contrary to previous reports of almost perfect compensation for head movements, we observed systematic errors for head roll but not for head translation. We explain these results by the fact that in our procedure slow feedback signals were not fully available. Inaccurate compensation might then reflect the slower integration of vestibular information for head roll than for head translation.

Acknowledgments

We are grateful to the members of the Centre Attention and Vision (AV, BS, DJ, EH, FP, JAG, MR, TBD and TK) and to Elodie Parison and Alice Szinte. This research was supported by a *Chaire d'Excellence* Grant to PC and a French *Ministère de l'Enseignement supérieur et de la Recherche* Grant to MS.

Corresponding authors

Correspondence should be addressed to Martin Szinte (martin.szinte@gmail.com), Laboratoire Psychologie de la Perception, Université Paris Descartes, CNRS – UMR 8158, 45, rue des Saints-Pères, 75006 Paris, France.

References

Angelaki, D. E., & Cullen, K. E. (2008). Vestibular System: The Many Facets of a Multimodal Sense. *Annual Review of Neuroscience*, *31*(1), 125–150.

Berthoz, A., Israël, I., Georges-Francois, P., Grasso, R., & Tsuzuku, T. (1995). Spatial memory of body linear displacement: what is being stored? *Science*, *269*(5220), 95 –98.

Bloomberg, J., Jones, G. M., & Segal, B. (1991). Adaptive modification of vestibularly perceived rotation. *Experimental Brain Research*, *84*(1), 47–56.

Blouin, J., Gauthier, G., van Donkelaar, P., & Vercher, J.-L. (1995). Encoding the position of a flashed visual target after passive body rotations. *Neuroreport*, *6*, 1165–1168.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.

Cullen, K. E. (2012). The vestibular system: multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences*, *35*(3), 185–196.

Duhamel, Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*(5040), 90–92.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences*, *103*(18), 7192–7197.

Gibson, J. J. (1950). *The perception of the visual world.* Oxford, England: Houghton Mifflin.

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Oxford, England: Houghton Mifflin.

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, *64*(2), 489–508.

Israël, I., & Berthoz, A. (1989). Contribution of the otoliths to the calculation of linear displacement. *Journal of Neurophysiology*, *62*(1), 247 –263.

Klier, E. M., & Angelaki, D. E. (2008). Spatial updating and the maintenance of visual constancy. *Neuroscience*, *156*(4), 801–818.

Klier, E. M., Angelaki, D. E., & Hess, B. J. M. (2005). Roles of Gravitational Cues and Efference Copy Signals in the Rotational Updating of Memory Saccades. *Journal of Neurophysiology*, *94*(1), 468 –478.

Klier, E. M., Hess, B. J. M., & Angelaki, D. E. (2006). Differences in the Accuracy of Human Visuospatial Memory After Yaw and Roll Rotations. *Journal of Neurophysiology*, *95*(4), 2692–2697.

Klier, E. M., Hess, B. J. M., & Angelaki, D. E. (2008). Human Visuospatial Updating After Passive Translations in Three-Dimensional Space. *Journal of Neurophysiology*, *99*(4), 1799–1809.

Li, N., & Angelaki, D. E. (2005). Updating Visual Space during Motion in Depth. *Neuron*, *48*(1), 149–158.

Medendorp, W. P., Smith, M. A., Tweed, D. B., & Crawford, J. D. (2002). Rotational Remapping in Human Spatial Memory during Eye and Head Motion. *The Journal of Neuroscience*, *22*(1), RC196.

Medendorp, W. P., Tweed, D. B., & Crawford, J. D. (2003). Motion Parallax Is Computed in the Updating of Human Spatial Memory. *The Journal of Neuroscience*, *23*(22), 8135 –8142.

Mergner, T., Nasios, G., & Anastasopoulos, D. (1998). Vestibular memory-contingent saccades involve somatosensory input from the body support. *NeuroReport*, *9*(7). Retrieved from http://journals.lww.com/neuroreport/Fulltext/1998/05110/Vestibular_memory_contingent_saccades_involve.41.aspx

O'Regan, J. K. (1992). Solving the "real" mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology/Revue canadienne de psychologie*, Object perception and scene analysis, *46*(3), 461–488.

Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Sperry, R. . (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of comparative and physiological psychology*, *43*(6), 482–489.

Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision*, *11*(2), 1–20.

Van Pelt, S., Van Gisbergen, J. A. ., & Medendorp, W. P. (2005). Visuospatial Memory Computations During Whole-Body Rotations in Roll. *Journal of Neurophysiology*, *94*(2), 1432–1442.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften*, *37*, 464–476.

Wei, M., Li, N., Newlands, S. D., Dickman, J. D., & Angelaki, D. E. (2006). Deficits and Recovery in Visuospatial Memory During Head Motion After Bilateral Labyrinthine Lesion. *Journal of Neurophysiology*, *96*(3), 1676–1682.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

4.4 Does remapping extend to extra-retinal space?

4.4.1. Objectives and summary of results

In this fourth study, we ask what happens to the representation of a target when remapping specifies a location outside the visual field, as would happen for any target near the edge of our visual field when we make a saccade away from that target. Will the target still have an active representation despite the extra-retinal location?

In the critical condition of the experiment, observers made a saccade between two fixation markers on a front screen while two probes were flashed sequentially at two locations on a side screen. The first probe was presented in the far periphery just within the observer's visual field. This target was extinguished and the observers made a large saccade away from the probe, which would have placed it outside the visual field if it had still been present. The second probe was then presented, displaced from the first in the same direction as the eye movement and by about the same distance as the saccade step. Because both eyes and probes shifted by similar amounts, there was little or no shift between the first and second probe positions on the retina. Observers reported that the probe appeared to move even though the first position fell, after an eye movement, outside the visual field. Interestingly, since the first and second presentations of the probes were chosen to fall at approximately the same retinal location (probe displacement matched saccade amplitude), the perception of motion suggests that apparent motion is computed in spatial, not retinal, coordinates (Rock & Ebenholtz, 1962). Importantly in this case, the pre-saccadic probe location must be remapped (Duhamel et al., 1992; Wurtz, 2008) to its expected post-saccadic location, prior to computing the motion, to a location outside the visual field. This suggests the existence of *visual* cells that represent extra-retinal space.

In three control conditions, we verified first that motion was reported between the two probes with the same displacement in the periphery when both probes and the remapped location of the first probe were all within the visual field. We then verified that observers do not see apparent motion when either the first or second probe was presented outside of the visual field demonstrating that we had accurately determined the extent of their visual field.

In the critical condition we found that observers do see apparent motion even when the location of the first probe lies outside the visual field. This study suggests that our model of shifting attention pointers driven by remapping (Cavanagh et al., 2010) must consider the possibility that the visuo-motor maps (e.g. LIP, FEF, SC) where remapping occurs, represent extra-retinal position. With this capability, attention pointers can predictively be placed at positions they would have after the saccade, even for extra-retinal locations.

Apparent motion from outside the visual field, retinotopic cortices may register extra-retinal positions

Article submitted to PLoS One

Martin Szinte[1,2] and Patrick Cavanagh[1,2]

Affiliations

1. Laboratoire Psychologie de la Perception,
   Université Paris Descartes, Sorbonne Paris Cité, Paris, France.
2. CNRS, UMR 8158, Paris, France.

Abstract

Observers made a saccade between two fixation markers while a probe was flashed sequentially at two locations on a side screen. The first probe was presented in the far periphery just within the observer's visual field. This target was extinguished and the observers made a large saccade away from the probe, which would have left it far outside the visual field if it had still been present. The second probe was then presented, displaced from the first in the same direction as the eye movement and by about the same distance as the saccade step. Because both eyes and probes shifted by similar amounts, there was little or no shift between the first and second probe positions on the retina. Nevertheless, subjects reported seeing motion corresponding to the spatial displacement not the retinal displacement. When the second probe was presented, the effective location of the first probe lay outside the visual field demonstrating that apparent motion can be seen from a location outside the visual field to a second location inside the visual field. Recent physiological results suggest that target locations are "remapped" on retinotopic representations to correct for the effects of eye movements. Our results suggest that the representations on which this remapping occurs include locations that fall beyond the limits of the retina.

Keywords

Visual field, remapping, saccade, extra-retinal space, apparent motion

Introduction

With our head and eyes steady, our normal binocular vision covers a visual field of about 200 to 220 degrees of visual angle (Harrington, 1981). In order to extend that limited area and mostly to bring several objects of interest to our central vision we frequently move our eyes and heads (up to 5 times per second for the eyes, see Rayner, 1998), abruptly shifting each time the projections on our retinas. Active cortical processes have been discovered in several visual areas (e.g., LIP, SC, FEF) that predict the retinal locations that attended objects will have following each eye movement (Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990; Gottlieb, Kusunoki, & Goldberg, 1998; Sommer & Wurtz, 2006; Walker, Fitzgibbon, & Goldberg, 1995). This visual areas are organized in retinotopic coordinates (Ben Hamed, Duhamel, Bremmer, & Graf, 2001; Sommer & Wurtz, 2000), so this updating process, called “remapping” (Duhamel et al., 1992), keeps track of target locations in the world despite the constant shifts on the retina. These processes may take advantage of a copy of the motor command for each eye movement (efference copy or corrolary discharge, Sommer & Wurtz, 2002; Sperry, 1950; von Holst & Mittelstaedt, 1950) to predict the new, post-saccadic target location.

In this paper, we ask what happens to the representation of a target when remapping specifies a location outside the visual field, as would happen for any target near the edge of our visual field when we make a saccade away from that target. Will the target still have an active representation despite the extra-retinal location? We can easily imagine that we maintain target representations in memory for objects we have seen but that are no longer in view (Curtis, Rao, & D’Esposito, 2004; Funahashi, Bruce, & Goldman-Rakic, 1989; Gnadt & Andersen, 1988). But we are not addressing whether visual memory encodes locations in general space around the body including behind the head, we are examining whether active perception itself does so. To test this, we will use a motion paradigm where observers report whether or not a probe appears to move even though one position falls, after an eye movement, outside the visual field.

We adapt a simple apparent motion task that we developed to assess the accuracy of the compensation (remapping) for saccades (Szinte & Cavanagh, 2011). In the original study, we presented two dots, one before and one after a horizontal saccade. Because of the eye movement, the two dots are separated by a large horizontal shift on the retina in addition to a vertical shift due to their actual displacement in the world. Despite this oblique displacement on the retina, participants reported seeing motion being close to vertical, almost as it is on the display monitor, demonstrating an efficient compensation for eye movements.

In our study here, we simply move the first dot to the edge of the visual field and follow it by a saccade away from its location. In order to update that location on a retinotopic representation, it must be remapped outside the visual field, because, if it were still present after the saccade, its location in space would now fall beyond the limit of the retina.

We reported here that observers do see apparent motion across a saccade even though its first location falls outside the visual field by the time the second position is presented. Since the first and second presentations are chosen to fall at approximately the same retinal location (probe displacement is matched to saccade amplitude), the perception of motion suggests that apparent motion is computed in spatial not retinal coordinates. This result has also been reported in several

previous articles (Fracasso, Caramazza, & Melcher, 2010; Rock & Ebenholtz, 1962; Szinte & Cavanagh, 2011) and it indicates that the compensation for the saccade must occur prior to the inference of motion. If this compensation or remapping (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Wurtz, 2008) occurs even when it would transfer activity to a location effectively outside the visual field, it could be evidence for the existence of *visual* cells that represent extra-retinal space.

Methods & apparatus

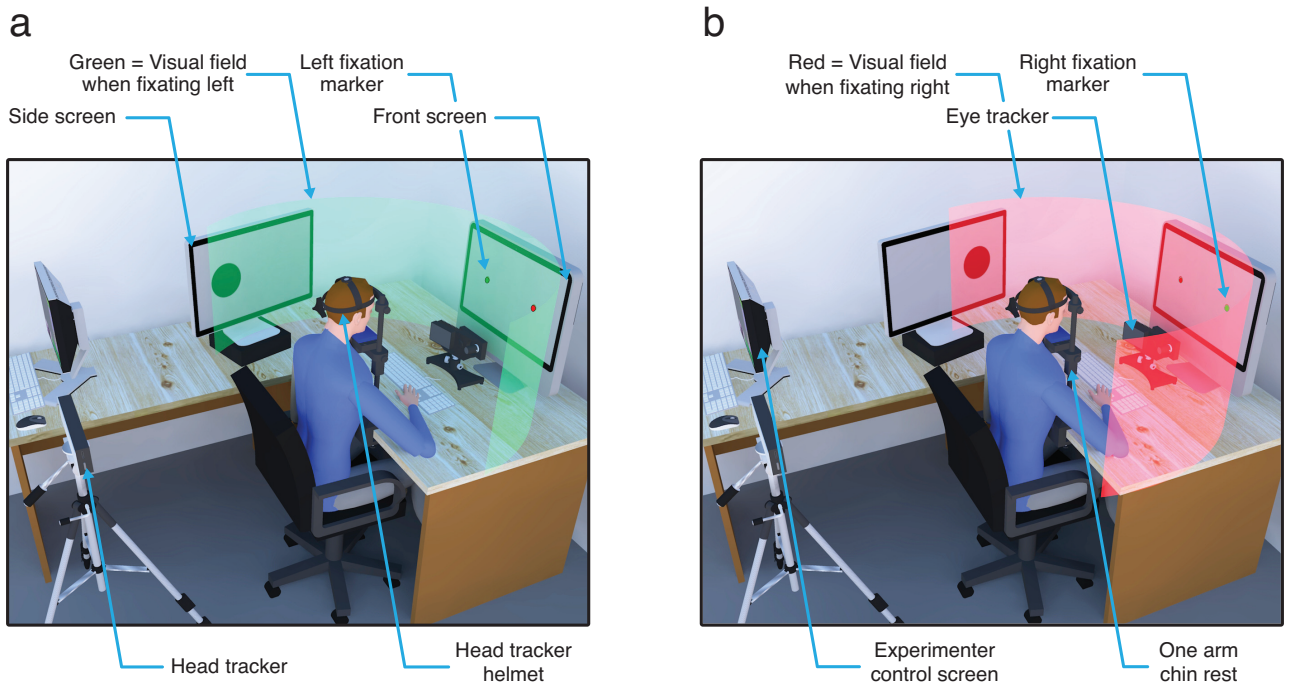


Figure 1. Apparatus and visual field. Two screens positioned at a distance of 60 cm from observers' head were used, a front screen displaying the fixation (green dot) and saccade (red dot) markers and a side screen displaying the apparent motion probes. Eye and head position are monitored using an eye tracker combined with a head tracker and a chin rest with the left support removed in order to leave the side screen visible. (a) The green parabolic field represents observer's visual field when fixating on the left fixation marker. The side screen is positioned such that the leftmost apparent motion probe falls just within the observer's visual field when he or she is fixating the left marker on the front screen. (b) The red parabolic field represents observer's visual field when he or she fixates the right fixation marker on the front screen. When fixating the rightmost marker, the right motion probe on the side screen falls at approximately the same position on the observer's retina as the left probe does when fixating the left marker, even though the two probes do not have the same position in space. Note, however, that the position of left motion probe falls outside observer's visual field when he or she fixates the right marker (at which time the left probe is no longer present).

Observers

Ten volunteers from Université Paris Descartes took part in the experiment (all observers were naïve to the purpose of the experiment, age 20-29 years, 4 males, and 6 females). All had normal or corrected-to normal vision and gave informed consent. The experiment was carried out according to ethical standards specified in the Declaration of Helsinki and was approved by the Ethics Committee from the Université Paris Descartes. All observers gave written informed consent before participating in the experiment.

Apparatus, instruments and stimuli

Observers were seated in a quiet, dimly lit room. Fixation markers were 1°-diameter green (30.0 cd/m^2) and red dots (30.0 cd/m^2) on a gray background (100 cd/m^2) presented on a gamma-linearized Apple iMac built-in 24" TFT display set 60 cm in front of observers' eyes (see "front screen" in Figure 1a). Apparent motion probes were 4º-diameter black dots (0.1 cd/m^2) on a gray background (100 cd/m^2) presented on a gamma-linearized Apple 24" LED-backlit TFT display placed in observers' left visual periphery (see "side screen" in Figure 1a) at a distance of 60 cm.

Both screens had identical screen resolution and size (1920 by 1200 pixels covering 48.89º by 30.56º each), as well as identical refresh rate (60 Hz). The experiment was controlled by an Apple iMac Intel Core 2 Duo computer. Manual responses were recorded via a standard keyboard. The dominant eye's gaze position was recorded and available online using an EyeLink 1000 Desktop Mounted (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. Three-dimensional head orientations as well as three-dimensional head spatial locations were recorded using a LaserBird optical motion tracker (Ascension Technology Corporation, Burlington, VT, USA), at a refresh rate of 60 Hz. This head tracker is composed of a lightweight sensor worn on a helmet held fixed to the back of the head and of a fan-shaped laser beam scanner positioned 60 cm below observer's head (see "head tracker helmet" and "head tracker" in Figure 1). The experimental software controlling the display, the response collection as well as the online eye and head tracking was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peter, & Palmer, 2002) and in-house head tracking toolboxes. Saccades were detected online when the gaze passed outside and landed later within virtual circles with a radius of 15% of the saccade amplitude (giving 3°; 3.75° or 4.5°-radius for 20°, 25° or 30° saccade trials) centered on the fixation and the saccade markers. Eye movement data were also re-analyzed offline based on eye velocity computed from subsequent samples in the eye position series (Engbert & Mergenthaler, 2006). The thresholds for peak velocity and minimum duration used for saccade detection were 3.0 SD and 20 ms. Head movement were detected online and trials were stopped and replayed later if observer's head orientation changed of ± 2.5 degrees of rotation (for either the yaw, roll or pitch angle) or if head position changed of ± 2.5 cm in any direction from an initial head calibration angles and locations.

Eye-head and secondary screen calibration

At the beginning of each experimental block, observers were asked to turn their heads in the central axis of the front screen. The head tracker provided the initial three-dimensional head orientation and spatial position values that were then used to detect any later head movement, as well as to positioned observers' head after any break. To help observers to maintain steady fixation, we used a chin rest that had only the right vertical support for the forehead brace so that the left support did not block the view of the side screen. Observers then executed a 13-point eye-tracking calibration in order to determine their gaze directions on the front screen. Then, we positioned the side screen such that its horizontal center fell 60 cm from observers' head and such that half of the side screen was located outside observers' left visual field when they correctly fixate at either 10°, 12.5° or 15° on the right side of the front screen center (see Figure 1b). To determine observer's left visual

field limit, we used a contrast detection task in which they had to report the contrast polarity, light or dark, of a 4°-diameter circle that could either be dark gray (25 cd/m^2) or light gray (175 cd/m^2) on a mid-gray background (100 cd/m^2). The probe was positioned 2° to the left of the side screen center and based on observers' discrimination, we moved the screen in order to increase or decrease the probe eccentricity. We stopped this procedure when observers said that they could not see anything on the side screen and when they were close to chance level on 20 consecutive trials (50 % ± 5 % correct). This adjustment procedure assured that observers were unable to see the left half of the side screen when they correctly fixated the right marker on the front screen (Figure 1b), although they can perfectly discriminate the probe contrast of that location on the left half of the side screen when fixating the left marker on the front screen (Figure 1a).

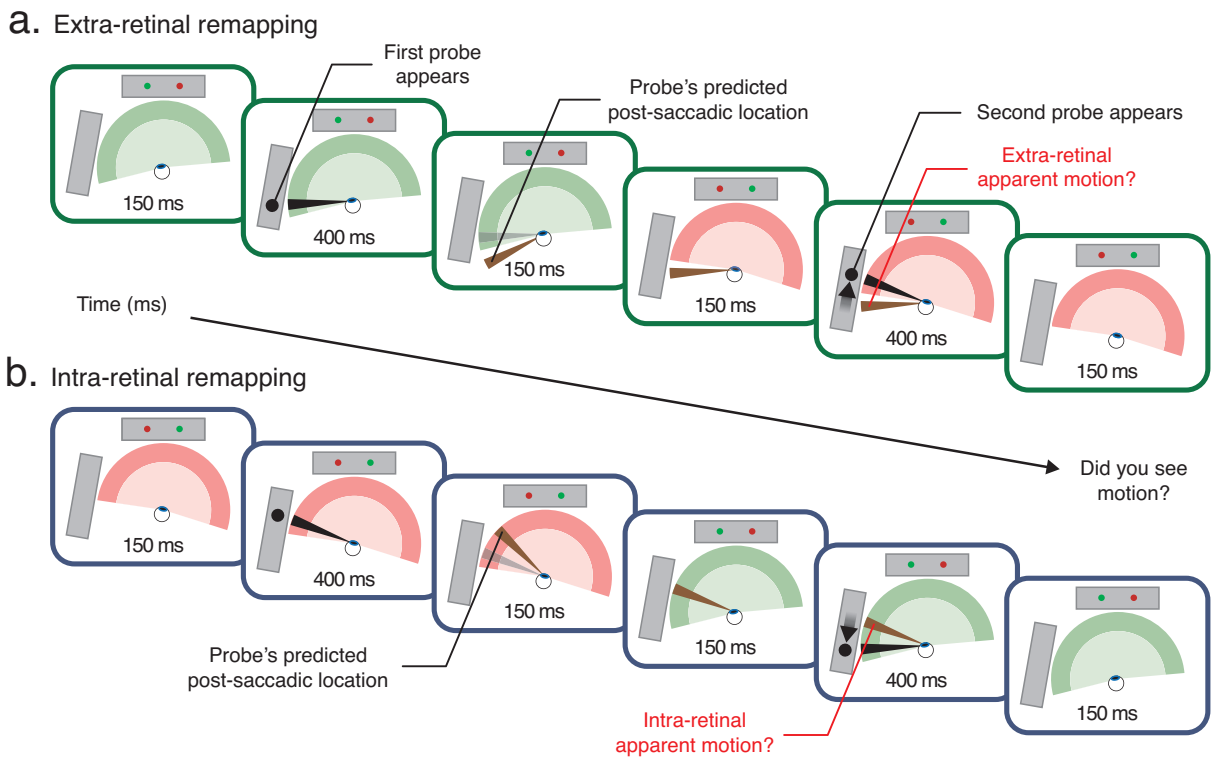


Figure 2. Stimulus sequence of the "intra-retinal" and "extra-retinal remapping" conditions. Each panel shows the sequence of the stimuli with a view from above the observer (represented by a single eye). The front screen and the side screen are shown as grey rectangles. The visual fields are shown as a green or red half circle when the observer fixates respectively the left or right fixation marker on the front screen. Each panel also represents the projections on the retina of the currently presented probe (black lines), of previously presented probe (gray lines) and of the predicted post-saccadic position of a probe (remapping) following the saccade (brown lines). (a) In the sequence of the extra-retinal remapping condition, probes were sequentially presented on the side screen, at the edge of observers' visual field, 150 ms before and 150 ms after the fixation markers exchange locations. Observers were instructed to follow the green fixation marker, making rightward saccades while the peripheral probe move in the same direction. Observers report after each trial whether they saw motion on the side screen. Probes distance matched the fixation markers distance, such that the two probes fell closely at the same position on the retina even if they had two distinct positions in space. Under these conditions, to perceive motion between probes, the first probe should be remapped at its post-saccadic position on the retina, falling then outside observer's visual field (see brown line), on extra-retinal visual space. (b) In the sequence of the intra-retinal remapping, observers made leftward saccades while probes moved in the same direction. The first probe is again remapped at its post-saccadic position, falling now inside observer's visual field, on intra-retinal visual space.

Experimental procedure

After the initial head and second screen calibration, all observers ran sequentially in a random order the 3 experimental conditions where the saccade amplitudes as well as the motion amplitudes vary between 20, 25 and 30°. Depending on the experimental condition, two fixation markers, one green and one red were presented at 10, 12.5 or 15° to the left and to the right of the front screen center, such that observers made horizontal saccades of either 20, 25 or 30°, selected equiprobably across trials. Observers were instructed to always fixate the green fixation marker and follow it as accurately as possible as it exchanged locations with the red one. The green fixation marker could appear at the beginning of a trial either on the left or the right of the front screen center, leading to equiprobable number of rightward and leftward saccade trials. Each trial began with the fixation marker filled with a smaller dark grey bull's-eye. When the observer's gaze was detected within a virtual circle centered on the fixation marker and if the head had not moved since the initial calibration, the bull's-eye changed from grey to orange. The orange dot indicated that correct fixation was achieved and that the trial would start momentarily. After 600 ms of correct fixation the marker was entirely filled with green and the trial began. Each trial was composed of three back and forth cycles where the red and green markers exchanged position every 700 ms. In the two first cycles nothing was presented on the second screen positioned to the left side of observers' eyes (side screen). This initial sequence helped observers to synchronize their saccades with the exchange of the two dots and to prepare themselves for the main cycle. In the main cycle, two apparent motion probes were presented sequentially on the side screen, one before and one after the saccade. Each probe was presented during 400 ms, with the first turned off 150 ms before the exchange of the green and red markers while the second turned on 150 ms later, giving then 300 ms for observers to complete their saccades. Probes were presented on the horizontal midline of the side screen and separated by the same offset as that between the fixation and saccade markers on that trial (20°, 25° or 30°). Finally, the order of appearance of these probes was equiprobably right-first or left-first, producing equal numbers of leftward and rightward motion trials. At the end of the main sequence, a red ring appeared around the green fixation marker indicating that the observers should report whether they saw or not any motion on the side screen.

Because the side screen was positioned in such a way that its left half could not be seen when the observers fixated at the right fixation marker of the front screen, the combination of the two saccade directions and the two motion directions give the four experimental conditions described in Figures 2 and 3.

In the first condition (Figure 2a), both the saccade and probes are displaced rightward. In order to predict the spatial position of the first motion probe following the saccade, its position is remapped by the amplitude of the saccade, but in the opposite direction (see Movie 1: http://cavlab.net/ExtraretinalMovies). The spatial location of the first probe should therefore be remapped outside of observer's visual field, if it can be. We called that condition, "*extra-retinal remapping*". Note in this case, that on the retina, both the first and second probe fall at approximately the same location at the edge of observer's visual field, one before and one after the saccade. The remapping is required to compute the retinal location where the first probe would have fallen after the saccade if it were still there, in order to detect any changes in its position that occurred at the same time as the saccade.

In the second condition (Figure 2b), observers executed a leftward saccade while motion probes

moved also leftward on the side screen (see Movie 2: http://cavlab.net/ExtraretinalMovies). Again to predict the spatial position of the first motion probe following the saccade, its position is remapped by the amplitude of the saccade but in the opposite direction. In this case the remapped location of the first probe now falls inside the observer's visual field. We therefore called this condition "*intra-retinal remapping*".

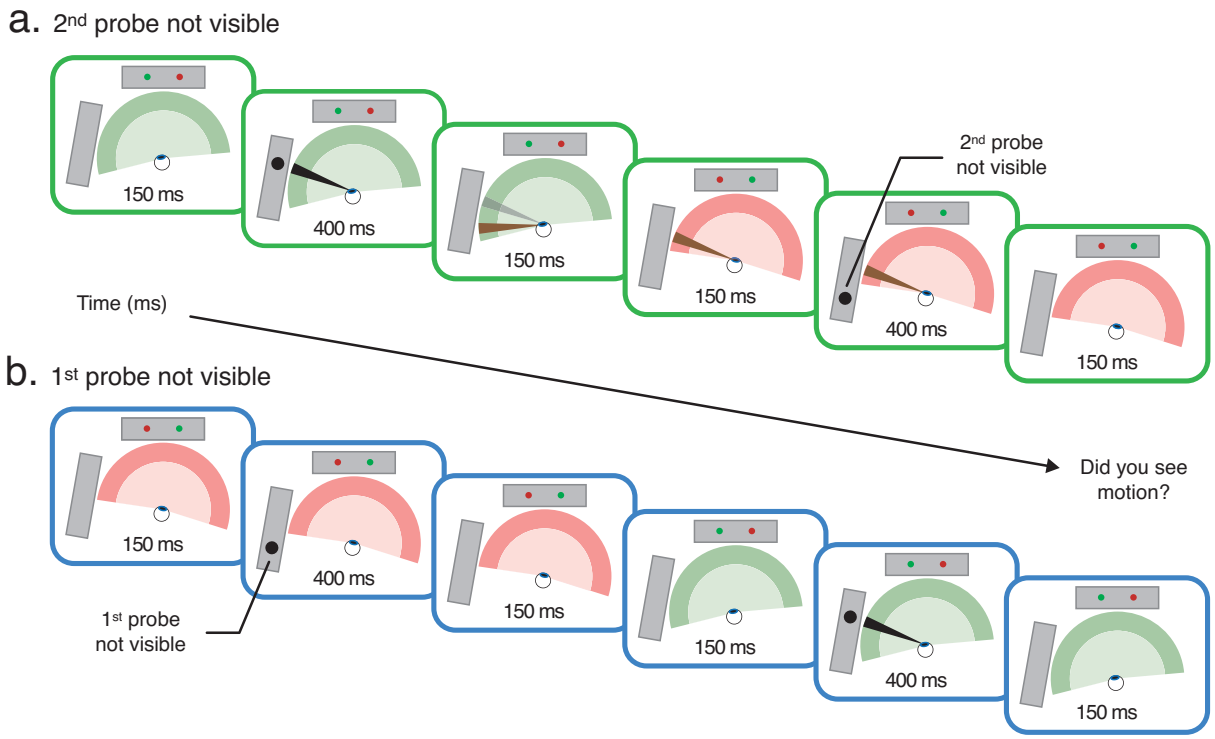


Figure 3. Stimulus sequence of the "2nd probe not visible" and "1st probe not visible" conditions. All conventions are the same as in Figure 2. These two control conditions tested whether we had properly positioned the side screen such that the left part of it lay outside observer's visual field when he or she fixated the right fixation marker. (a) In the sequence of the "2nd probe not visible" condition, observers made rightward saccade while probes on the side screen moved in the opposite direction (leftward). Although the first probe location fell inside observers' visual field and may have been remapped (brown line), the second probe fell outside observer's visual field, such that no motion could be perceived after the saccade. (b) In the sequence of the "1st probe not visible" condition, observers made leftward saccade while probes moved rightward. Then, the first probe appeared outside of observer's visual field such that no motion could be perceived after the saccade.

In the third condition (Figure 3a), called "*2nd probe not visible*" condition, the saccade goes rightward while probes moved leftward on the side screen (see Movie 3: http://cavlab.net/ExtraretinalMovies). In this case, although the first probe location may have been remapped, the second probe falls outside observer's visual field, and thus no motion should be perceived after the saccade, testing whether we had properly positioned the side screen and thus the position of the probes. Finally, in the fourth condition (Figure 3b), called "*1st probe not visible*", observers executed a leftward saccades but this time the motion probes moved rightward on the side screen (see Movie 4: http://cavlab.net/ExtraretinalMovies). In this case, the first motion probe appeared outside of the observer's visual field and thus no motion should be perceived after the saccade (again testing whether we had properly positioned the side screen).

Results

We evaluated the proportion of motion reports for the 4 experimental conditions (described above) for all saccade amplitudes tested. When inaccurate saccade trials or trials where head movement exceeded our criteria from the initial head calibration position were detected on line, they were rejected and replaced (305 trials repeated out of 2705 trials played, giving 2400 selected trials). We then re-analyzed the eye-tracking data offline in order to select only trials where the motion probes were presented trans-saccadically. We thus looked for trials in which the saccade started after the first probe offset and ended before the second probe onset. Within addition we also rejected trials with blinks and those that failed a finer offline evaluation of saccade accuracy. This correction led us to reject a further 548 trials, leaving 77.2% of selected trials (1852/2400; corresponding to 68.5% of all trials). Note that maintaining a steady head position was not a major source of trial rejections as 84.7 % of the rejections were due to saccades occurring too early (476 of 562 rejected trials). The screening left an average of 185 ± 16 trials per observer, ranging from 45.4% (GL: 109/240) to 97.9% (JT: 235/240).

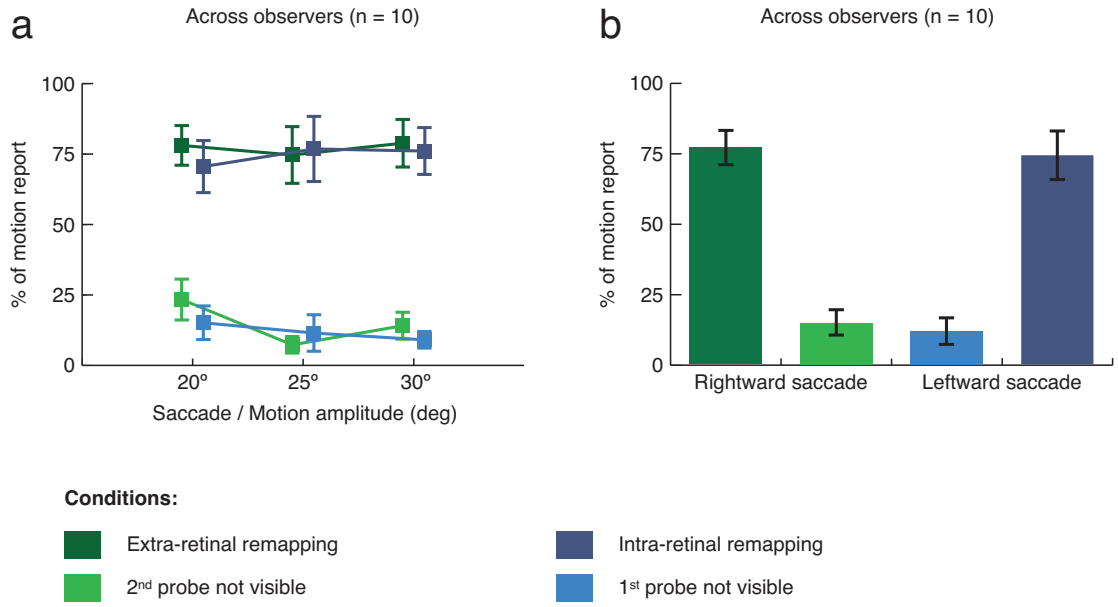


Figure 4. Group results. (a) The left panel shows the average (n = 10) percentage of motion report for the 4 experimental conditions and the three saccade and motion amplitudes tested. (b) The right panel shows the same data but this time collapsed across the three saccades and motion amplitudes tested. Error bars in both panels represent SEM across observers.

Figure 4a shows the proportion of motion reports for the four experimental conditions and the three different saccade/motion amplitudes. A repeated measures ANOVA (with experimental conditions and saccade amplitudes as main factors), shows a main effect of experimental condition ($F(3,27) = 40.74$, $p < 0.001$) and no effect of the saccade amplitude ($F(2,54) = 0.67$, $p = 0.52$). There is no significant interaction between these variables ($F(6,54) = 0.92$, $p = 0.49$). We therefore collapsed our data across the different saccade amplitudes (Figure 4b). In both “extra-retinal” and “intra-retinal remapping” conditions observers report seeing motion on the side screen in 3 trials out of 4, with 77.3% ± 6.1% and 74.5% ± 8.5% of motion report across all observers for “extra-retinal” and “intra-retinal remapping” tests respectively (no significant difference between the two conditions, $F(1,9) = 0.39$, $p = 0.55$). These results are significantly different from the control conditions ($F(1,9) = 47.11$, p

< 0.001), where motion was reported in about 1 or 2 trials out of 10, 15.0% ± 4.6% and with 12.0% ± 4.8% of motion report across observers for "2nd probe not visible" and "1st probe not visible" condition respectively (no significant difference between the two control conditions, $F(1,9) = 1.22$, $p = 0.30$).

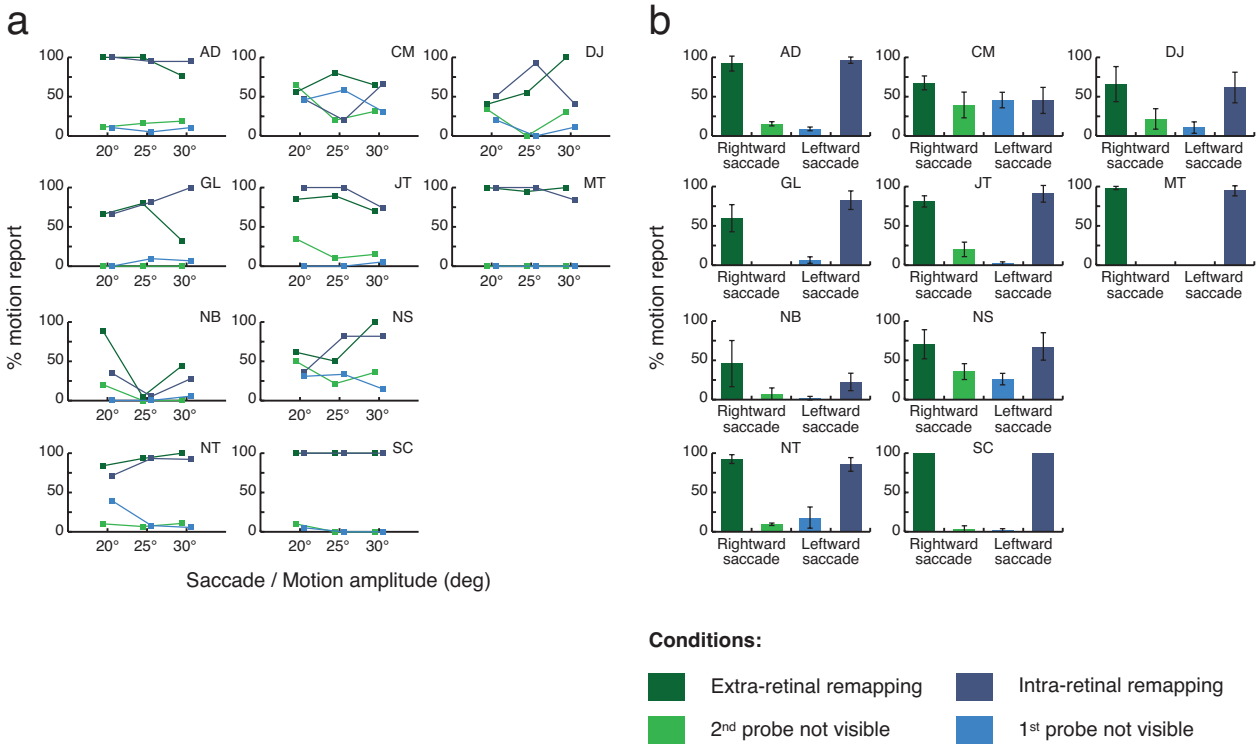


Figure 5. Individual results. This figure shows (a) for each observer (in columns and rows), the percentage of motion report for the four experimental conditions and the 3 saccade and motion amplitudes tested and (b) these same data collapsed across saccade amplitudes. Error bars in panel (b) represent SEM across the 3 saccade and motion amplitude tested.

Next, we determined whether the pattern seen across observers also held in individual results. Figure 5 shows the proportion of motion reports across our four experimental conditions and saccade/motion amplitudes for each observer individually (see Figure 5a), as well as the same data collapsed across saccade amplitudes (see Figure 5b). Individual data are similar to group results across 8 of the 10 observers. Two observers, CM and NB, showed qualitatively different results. CM reported motion even when only one dot should have been seen. An error in locating the edge of the visual field at the beginning of the experiment might have made both probes visible in all conditions. However, when asked at the end of the experiment CM explained that she experienced motion even when she saw only a single dot. In that case she perceived motion as briefer and of shorter amplitude than when she saw two dots, but reported it as motion nonetheless. On the other hand, NB rarely reported seeing motion in any condition. At the end of the experiment, we asked her to report if she saw apparent motion when the probes were displaced while she maintained fixation at the left marker (so that both probes were visible and moved without any intervening saccade). Interestingly, she didn't report seeing motion suggesting that the distance between probes might have been too large or the delay between the two probes to long for her to see motion.

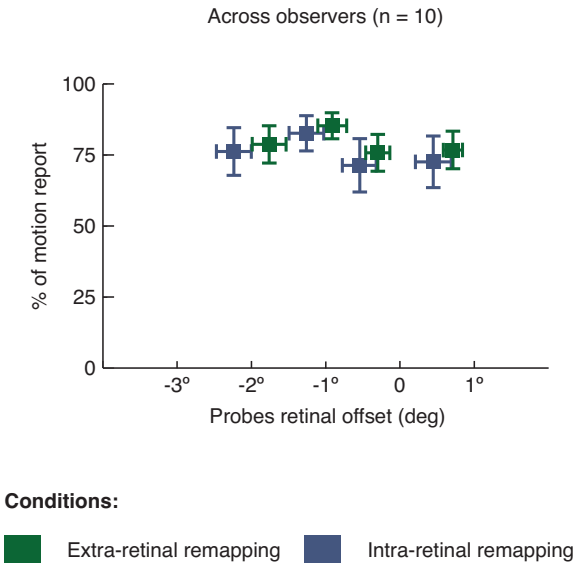


Figure 6. Effect of retinal offset between the two probes. This graph shows the proportion of motion reports for the retinal offset between the two probes (in quartile bins) for 2 experimental conditions where two probes were visible, averaged across observers (n = 10). With the head steady and the intended amplitude of the saccade (20, 25 or 30°) matching the amplitude between probes on the side screen, the two probes should fall on the same location on the observers' retina. There is, however, a retinal offset that results from under- or overshoot of the saccade. As seen here, saccades generally landed short of the fixation target, leading to a retinal offset between -2 and +1 degrees. However, this retinal offset had no effect on observers' motion reports. This is especially interesting for offsets around 0° when both probes stimulate almost the same retinal location (third quartile). Here observers report seeing motion across the saccade in both the extra and intra retinal remapping condition despite the lack of shift on the retina. Horizontal error bars represent SEM across observers for the retinal offset, while the vertical bars represent SEM across observers for the motion report.

Finally, we were interested to test if apparent motion could be seen when the same location on the retina was stimulated by the first and second probe when a saccade intervened. This duplicated Rock & Ebenholtz's (1962) demonstration of motion reports when a stimulus landed on the same retinal location before and after a saccade, although in our case, these locations are now in the far periphery. There, as here, observers reported seeing motion (see Figure 6) indicating that the location of the pre-saccadic probe was corrected for the saccade so that a large offset in space was seen rather than the null offset on the retina. Figure 6 shows the proportion of motion report for 4 quartiles bins of probes retinal offset in function of the 2 experimental conditions where two probes were visible. For the two experimental conditions separately, the proportion of motion report is very similar between the four different quartiles (ANOVA with motion shift quartiles and experimental condition as main factors shows no main effect of motion shift, $F(3,63) = 1.01$, $p = 0.40$). Critically, in both the extra and intra-retinal remapping conditions, when the probes' retinal offset was around 0° (third quartile in Figure 6, retinal offset between -0.28° ± 0.16° and -0.58° ± 0.24° respectively), observers still reported seeing motion with, respectively, 75.8% ± 6.5% and 71.4% ± 0.2% of motion report across all observers. This last result shows that even when both probes stimulate approximately the same retinal location, observers report seeing motion across saccades. This indicates, as Rock and Ebenholtz (1962) first reported, that apparent motion is seen in spatial coordinates, not retinal coordinates.

Discussion

We used sequential probes with an intervening saccade to determine whether apparent motion was seen in spatial not retinal coordinates at the edge of the visual field. Critically, in one condition, the first probe fell within the visual field only when it was first presented, but its location then fell outside the visual field after the saccade. Nevertheless, on 75% of trials, motion was seen after the saccade from this extra-retinal location to a new location within the visual field, indicating that the visual system keeps track of locations that move outside the visual field due to saccades. Motion was also seen at the same rate (75% of trials) when the first probe location still fell within the visual field after the saccade.

Apparent motion was reported in these conditions even though the size of the saccades and the displacement of the probes were matched to produce, ideally, no displacement on the retina. In fact, of course, saccade may under- or overshoot but when we analyzed the frequency of motion reports, it was constant, independent of the actual small offset on the retina (from -2° to +1°) caused by inaccurate saccade landings, including the small range around no displacement. This result replicates the finding of Rock & Ebenholtz (1962) demonstrating that apparent motion is determined in spatial not retinal coordinates.

In the remaining two conditions, either the first or second probe fell outside the visual field when it was presented and should have been invisible. The frequency of motion reports here was much lower (12 to 15%) indicating that our original calibration to locate the edge of the visual field was accurate.

Our results show that objects that move in the world are seen to move even if there is no displacement on the retina (Rock & Ebenholtz, 1962). This indicates that the pre-saccadic location of the first probe is corrected for the effects of the saccade prior to the determination of apparent motion between the two locations. This correction removes the most of the effect of the saccade from the perceived motion direction (but not all, see Szinte & Cavanagh, 2011). The possible mechanisms for this compensation include “remapping” based on efference copy (Cavanagh et al., 2010; Sperry, 1950; von Helmholtz, 1867; von Holst & Mittelstaedt, 1950; Wurtz, 2008). In our displays, when a probe is near the limit of the visual field and the saccade moves away from the probe, its predicted post-saccadic location is remapped outside the visual field, requiring extra-retinal representation. Apparent motion is then seen from this predicted post-saccadic location to the new probe location, back within the visual field. To explain our results, the representation would have to extend at least 15 degrees of visual angle outside the visual field. The representation of the far periphery (from 80 to 100°) covers very little cortical surface (Daniel & Whitteridge, 1961) so the extra 15° would take up even less. Indeed, in an fMRI study by Tark & Curtis (2009) a persistent neural activity have been shown in FEF for memorized auditory stimuli presented in extra-retinal visual space, that is to location where no saccade could have been made.

Alternate proposals for saccadic correction when applied to our probes in the far periphery would also lead to a requirement for extra-retinal representation. For example, with “reference object theory,” a memory of the saccade target landscape is used to locate the original saccade goal so that no efference copy is needed to predict its location (Bridgeman, Van der Heijden, & Velichkovsky,

1994; Deubel, Bridgeman, & Schneider, 1998; Deubel, Koch, & Bridgeman, 2010; Koch & Deubel, 2007). Since this process only involves the saccade target, other targets like our motion probes would have to be localized relative to the saccade target. After the saccade is made, the relative offset from the saccade target to the first probe then specifies a location outside the visual field. When the second probe appears at a new location, apparent motion is seen from the first position (outside the visual field) to the second.

In our procedure, we used apparent motion, a type of visual motion that for large displacements cannot be explained by simple motion receptors (Cavanagh & Mather, 1989) and that is best described as an attentional phenomenon (Cavanagh, 1992; Wertheimer, 1912). As Wertheimer (1912) described it, a probe first attracts attention to one location followed by a second probe that drags attention to its new location, giving a strong impression of motion. In the case of trans-saccadic apparent motion, attention would be first remapped to the expected post-saccadic location of the first probe, then when the second probe appears at a different location, attention is dragged to that new location even though the two probes were matched in retinal coordinates. This creates apparent motion in a spatiotopic reference frame (Fracasso et al., 2010; Szinte & Cavanagh, 2011), supporting Rock and Ebenholtz's (1962) earlier report.

The perceptual effect we report differs from the more general ability to remember the location of an object previously seen but no longer visible. In our case the perception of motion suggests that basic visual representations of location underlie the effect rather than memory of location. Even without intervening saccades and possible extra-retinal locations, apparent motion is not seen for probe-to-probe intervals beyond about 400 ms (Caelli & Finlay, 1979) indicating that visual memory alone cannot produce apparent motion phenomena.

Our results suggest that positions outside the visual field are coded in saccade and attention maps, however, we cannot determine in this experiment whether the effective extra-retinal location actually corresponds to the spatial location of the first probe. Alternatively, all remapping or predicted locations that would lie beyond the edge of the visual field may simply be referred to the edge of the visual field. In this case, our stimuli would give an impression of a motion path half as long as the actual path. In a follow up experiment, we plan to ask observers to report the length of the motion path, and point to the first dot location to determine if there is any compression of locations at the edge of the visual field.

Conclusion

We show here that the perception of motion is reported between two probes when a saccade intervened between the presentation of the first and second probe, even though, in some conditions, when the second probe was presented, the effective location of the first probe lay outside the visual field. This result suggests that apparent motion can be seen from a location outside the visual field to a second location inside the visual field. The probe locations were arranged so that the shift between two distinct positions in space caused them to fall at approximately same position on the retina. The fact that apparent motion was seen under these conditions indicates that the motion is seen in spatial not retinal coordinates (Rock & Ebenholtz, 1962) and that therefore, the pre-saccadic probe location

must be corrected for the effect of the saccade before the computation of the motion. This correction or "remapping" (Cavanagh et al., 2010; Duhamel et al., 1992; Wurtz, 2008) would place the expected post-saccadic location of the first probe outside the visual field.

Our interpretation rests on the subjective motion reports of our observers. In both conditions where the first and second probes are presented within the visual field, observers report motion on about 75% of the trials and this figure is unaffected by whether the first probe's location lies outside the visual field after the eye movement. So we believe that observers are reporting the phenomenal experience of motion, as requested, and not just reporting the displacement of the perceived (and remembered) locations. Displacement reports (not based on motion) would have reached 100% in these conditions with both probes visible. We do not believe that the eye movement itself is triggering a percept of motion as the great majority of cases with one of the two probes not visible led to reports of no motion.

Nevertheless, it is clear that this is only a first evaluation of extra-retinal motion percepts and that further studies that go beyond these subject motion reports are needed. If our first results here hold up, it suggests that areas representing visual stimuli in retinotopic coordinates have cells that respond to extra-retinal space, beyond the margins of the visual field. These cells keep track of targets that have just moved outside the visual field. If these stimuli then move to return to our field of view, we see them not as simply reappearing but as moving.

Acknowledgments

We are grateful to the members of the Centre Attention and Vision (AV, BS, DJ, EH, FP, JAG, MR, SC, TBD and TK) and to Elodie Parison and Alice Szinte. This research was supported by a *Chaire d'Excellence* Grant to PC and a French *Ministère de l'Enseignement supérieur et de la Recherche* Grant to MS.

Corresponding authors

Correspondence should be addressed to Martin Szinte (martin.szinte@gmail.com), Laboratoire Psychologie de la Perception, Université Paris Descartes, CNRS – UMR 8158, 45, rue des Saints-Pères, 75006 Paris, France.

References

Ben Hamed, S., Duhamel, J.-R., Bremmer, F., & Graf, W. (2001). Representation of the visual field in the lateral intraparietal area of macaque monkeys: a quantitative receptive field analysis. *Experimental Brain Research*, *140*(2), 127–144.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A Theory of Visual Stability Across Saccadic Eye Movements. *Behavioral and Brain Sciences*, *17*(02), 247–258.

Caelli, T., & Finlay, D. (1979). Frequency, phase, and colour coding in apparent motion. *Perception*,

8(1), 59–68.

Cavanagh, P. (1992). Attention-based motion perception. *Science*, *257*(5076), 1563–1565.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*(2), 103–129.

Cornelissen, F. W., Peter, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617.

Curtis, C. E., Rao, V. Y., & D'Esposito, M. (2004). Maintenance of Spatial and Motor Codes during Oculomotor Delayed Response Tasks. *The Journal of Neuroscience*, *24*(16), 3944 –3952.

Daniel, P. M., & Whitteridge, D. (1961). The representation of the visual filed on the cerebral cortex in monkeys. *The Journal of Physiology*, *159*, 203–221.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research*, *38*(20), 3147–3159.

Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Research*, *50*(2), 249–259.

Duhamel, Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*(5040), 90–92.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences*, *103*(18), 7192–7197.

Fracasso, A., Caramazza, A., & Melcher, D. (2010). Continuous perception of motion and shape across saccadic eye movements. *Journal of Vision*, *10*(13), 1–17.

Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*, *61*(2), 331 –349.

Gnadt, J., & Andersen, R. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Experimental Brain Research*, *70*(1), 216–220.

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, *64*(2), 489–508.

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, *391*(6666), 481–484.

Harrington, D. O. (1981). *The Visual Fields: A Textbook and Atlas of Clinical Perimetry*. St. Louis, MO: Mosby.

Koch, C., & Deubel, H. (2007). How postsaccadic visual structure affects the detection of intrasaccadic target displacements. In R. P. G. van Gompel, M. H. Fisher, W. S. Murray, & R. L. Hill (Eds.), *Eye movements: A window on mind and brain.* (pp. 193–212). Oxford,UK: Elsevier.

Pelli, D. G. (1997). The Video Toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*(3), 372–422.

Rock, I., & Ebenholtz, S. (1962). Stroboscopic movement based on change of phenomenal rather than retinal location. *The American Journal of Psychology*, *75*(2), 193–207.

Sommer, M. A., & Wurtz, R. H. (2000). Composition and Topographic Organization of Signals Sent From the Frontal Eye Field to the Superior Colliculus. *Journal of Neurophysiology*, *83*(4), 1979–2001.

Sommer, M. A., & Wurtz, R. H. (2002). A Pathway in Primate Brain for Internal Monitoring of Movements. *Science*, *296*(5572), 1480–1482.

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*(7117), 374–377.

Sperry, R. . (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of comparative and physiological psychology*, *43*(6), 482–489.

Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision*, *11*(2), 1–20.

Tark, K.-J., & Curtis, C. E. (2009). Persistent neural activity in the human frontal cortex when maintaining space that is off the map. *Nature Neuroscience*, *12*(11), 1463–1468. doi:10.1038/nn.2406

von Helmholtz, H. (1867). *Handbuch der physiologischen Optik*. Leipzig: Voss.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften*, *37*, 464–476.

Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology*, *73*(5), 1988–2003.

Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie*, *61*, 161–165.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

4.5 The peri-saccadic allocation of attention

4.5.1. Objectives and summary of results

Remapping has been shown to occur for attended targets (Gottlieb et al., 1998). A recent study showed that remapping can be seen in humans as a pre-saccadic allocation of spatial attention to the remapped location (Rolfs et al., 2011). In contrast, after a saccade, previous work has suggested that attention is maintained at the retinotopic location (known as the retinotopic trace of attention) of a pre-saccadic attended object, and that it is less evident at the attended object's location in space where the remapped activation should have brought it (Golomb et al., 2008). In this last study we tracked the allocation of attention both before and after saccades within the same experiment. We also investigated another strategy that the visual system may rely on to localize objects after the saccade: a search for visual features (such as object shape or color), which could contribute to spatial attention shifts after the saccade.

While observers prepared a saccade, we presented an irrelevant but salient color cue in the observer's visual periphery, drawing visual attention (but not the eyes) to the cued location. We evaluated the attentional benefits, if any, at each location using a fine orientation discrimination task in which observers reported the tilt of a close-to-vertical Gabor, briefly presented at different times before and after the saccade. We examined three positions of interest: the location of the cue, a location offset from the cue in the direction of the saccade (future retinotopic trace) and a location offset from the cue in the direction opposite to the saccade (remapped location), that is, the future retinal position of the cue. In addition, there were three corresponding control locations, mirrored with respect to the saccade vector. Using this design, we were able to determine whether spatial attention is remapped before the saccade, and whether, after the saccade, spatial attention is seen at the cued location in space or, if instead it persists at the location on the retina where the cue appeared.

Before saccade onset, we found the expected rise in performance at the cue location indicating a strong allocation of attention drawn by the transient onset of the cue. Critically, this benefit was maintained at the spatial location of the cue after the saccade, without showing the temporary loss that would arise if the visual system had to locate the cue location anew. We attribute this spatiotopic benefit, seen following the saccade, to the attention that had been allocated to the remapped location of the cue just prior to the saccade. This remapped location corresponds to the retinal location that would align with the cue when the eyes land. As proposed earlier (Berman & Colby, 2009; Hall & Colby, 2011; Wurtz, 2008), an efference copy of the upcoming saccade is used to shift the attention that was attracted to the cue to the location the cue will have after the saccade. The eye movement then shifts this attentional focus or "pointer" into place at the cue's location after the saccade, effectively updating the cue's "attention pointer" (Cavanagh et al., 2010).

After the saccade, we also observed an attentional benefit at the retinal location that the cue occupied before the saccade. This retinotopic trace of attention (Golomb et al., 2008) is short-lived and observed only for the first 100 ms following the saccade, suggesting a decay of activity in retinotopic neural populations processing the cue before the saccade.

To disentangle the role of spatial attention and feature-search effects across saccades, we also manipulated the presentation duration of the cue. In one condition (Transient-cue), the cue appeared before and disappeared during the saccade. In a second condition (Sustained-cue), the cue remained present for the whole duration of the trial. When the cue remained present after the saccade, it could have contributed to the post-saccadic allocation of attention, whereas in the latter it could not. We found that, immediately after the saccade, spatial attention was allocated to the correct position of the cue in space whether or not the color was still there. This finding suggests that attentional benefits at the cue location after the saccade mainly depend on the predictive updating of locations of interest.

Overall, our results portray a dynamic picture of attention allocation before and after saccadic eye movements. Attention drawn to salient objects before a saccade is remapped around the time that the eyes move. As a consequence, attention is maintained at the spatial locations of attended objects in the world, correcting for the large position shifts that eye movements cause on the retina and throughout retinotopic cortices.

These results, together with a previous report of the attentional remapping of potential saccade targets (Rolfs et al., 2011), strongly support our model of space constancy based on a transfer of attention pointers preceding the consequences of eye movements (Cavanagh et al., 2010).

Allocation of attention across saccades

Article submitted to Journal of Neurophysiology

Donatas Jonikaitis[1,2,3], Martin Szinte[2,3], Martin Rolfs[4] and Patrick Cavanagh[2,3]

Affiliations

1. Allgemeine und Experimentelle Psychologie,
   Ludwig-Maximilians-Universität München, Munich, Germany.
2. Laboratoire Psychologie de la Perception,
   Université Paris Descartes, Sorbonne Paris Cité, Paris, France.
3. CNRS, UMR 8158, Paris, France.
4. Laboratoire de Psychologie Cognitive,
   Université Aix-Marseille & CNRS, Marseille, France.

Abstract

Whenever the eyes move, spatial attention must keep track of the locations of targets as they shift on the retina. This study investigated trans-saccadic updating of visual attention to cued targets. While observers prepared a saccade, we flashed an irrelevant, but salient color cue in their visual periphery and measured the allocation of spatial attention before and after the saccade using a tilt discrimination task. We found that just before the saccade, attention was allocated to the cue's future retinal location, its predictively "remapped" location. Attention was sustained at the cue's location in the world across the saccade, despite the change of retinal position whereas it decayed quickly at the retinal location of the cue, after the eye landed. By extinguishing the color cue across the saccade, we further demonstrate that the visual system relies only on predictive allocation of spatial attention, as trans-saccadic feature changes in the cue do not substantially affect attentional allocation. These behavioral results support and extend physiological evidence showing predictive activation of visual neurons when an attended stimulus will fall in their receptive field after a saccade. Our results show that tracking of spatial locations across saccades is a viable function of physiological remapping.

Introduction

The average inter-saccadic interval is short, about 1/3 of a second, so in everyday situations, we view, study, recognize, and track objects across many fixations. Each object is therefore encoded from several locations on the retina and then processed at various times by several different sets of neurons in retinotopic visual processing areas (Gardner, Merriam, Movshon, & Heeger, 2008; Sereno et al., 1995). Clearly, every time we make an eye movement, the visual system needs to account for retinal image shifts to maintain object continuity as well as the stability of our visual world (Wurtz, 2008).

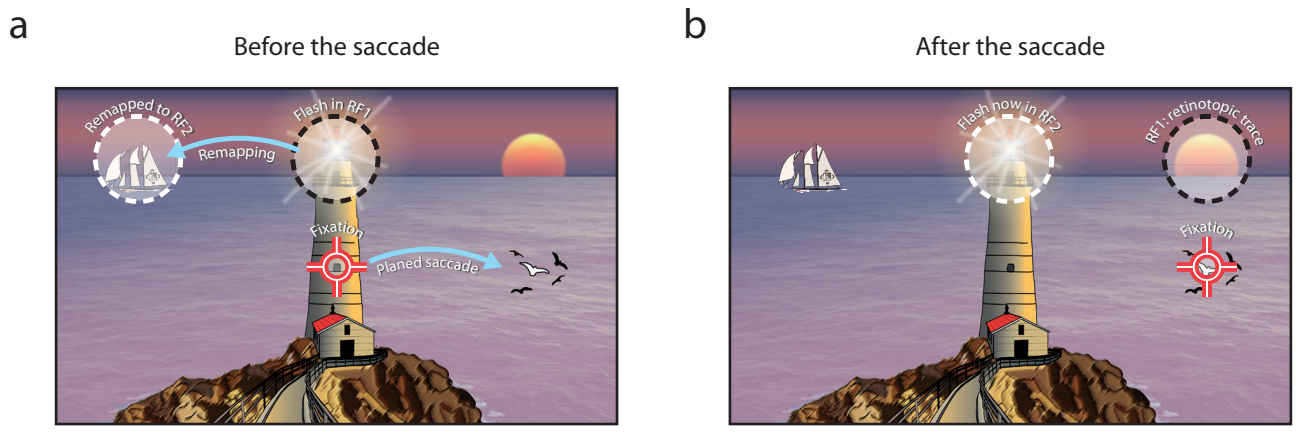


Figure 1. Predictive remapping. While the observer is preparing a saccade from the lighthouse window to the white bird, a flash captures their attention. This flash is registered by a population of neurons with receptive fields at that location (RF1: black dashed circle in panel a). However, after the saccade, receptive fields of those neurons are at an irrelevant location; corresponding to the retinotopic trace of the flash (RF1: black dashed circle in panel b). To keep track of this potentially relevant visual event, the visual system needs to relocalize, or remap, the attention captured by the flash to the retinotopic location the flash will have after the saccade. This remapping aids visual stability by pre-activating, before and during the saccade, a population of neurons with receptive fields at the retinal location (RF2: white dashed circle in panel a) which will match the location of the flash after the saccade (RF2: white dashed circle in panel b).

Physiological research suggests that saccade control areas may compensate for the retinal image shifts caused by eye movements (Duhamel, Colby, & Goldberg, 1992; Hall & Colby, 2011; Kusunoki & Goldberg, 2003; Sommer & Wurtz, 2002). Post-saccadic target location is determined by taking into account pre-saccadic target position and the metrics of the planned saccade. This results in the shift of neural activity from neurons with receptive fields encoding the pre-saccadic target position to neurons with receptive fields encoding its post-saccadic position (Figure 1), an effect called remapping (Duhamel et al., 1992; Heiser & Colby, 2006; Nakamura & Colby, 2002; Sommer & Wurtz, 2002). In some areas, remapping is even observed before the saccade (Duhamel et al., 1992; Kusunoki & Goldberg, 2003). Remapping-related neural activity has also been demonstrated in humans (Medendorp, 2011; Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003; 2007; Parks & Corballis, 2008; 2010). Because of the close link between activity in saccade control areas and spatial attention (Awh, Armstrong, & Moore, 2006; Bisley & Goldberg, 2010; Moore & Armstrong, 2003; Schall, 2004), we can track remapping with behavioral tests of attention benefits (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011).

However, most of the studies investigating visuospatial updating have focused on either pre-saccadic or peri-saccadic intervals (Duhamel et al., 1992; Heiser & Colby, 2006; Nakamura & Colby, 2002; Sommer & Wurtz, 2002). The assumption that perceptual processing benefits seen at the remapped location before the saccade (Rolfs et al., 2011) are transferred to the spatial location of the cue after the saccade, has not yet been tested. Some studies of attentional cueing using targets presented following the saccade have actually reported retinotopic, not spatiotopic, perceptual benefits (Golomb, Chun, & Mazer, 2008; Golomb, Marino, Chun, & Mazer, 2011; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b). However, those studies investigated updating of memorized locations, a process which likely has a different time course than the remapping of stimuli present in the immediate visual environment (see Golomb et al., 2008 for discussion). Thus, it is unknown whether predictive remapping can be associated with spatiotopic allocation of attention across saccades.

Additionally, most remapping studies investigated updating of spatial locations, without respect to object features or identity (Duhamel et al., 1992; Hall & Colby, 2011; Medendorp et al., 2003; Merriam et al., 2003; Nakamura & Colby, 2002; Parks & Corballis, 2010; Sommer & Wurtz, 2002). Remapping provides a predicted post-saccadic location for attended objects but the prediction may have some error (Szinte & Cavanagh, 2011) and objects may move during a saccade. An auxillary method to establish target locations can call on checking for whether post-saccadic object features match those stored in the trans-saccadic memory (Crapse & Sommer, 2012; Deubel, Bridgeman, & Schneider, 1998; Deubel, Koch, & Bridgeman, 2010; Deubel, Schneider, & Bridgeman, 1996). This process may take some time after the saccade (Zhou & Desimone, 2011), but would be a viable strategy if spatial updating after the saccade is slow (Golomb et al., 2008). However, neither the timing, nor the relative contributions of spatial remapping and feature matching processes after the saccade is known.

In the current study, we devised a task to investigate these two issues (Figure 2). While participants planned a saccade, we induced attentional capture with the onset of an irrelevant color cue (Carrasco & Yeshurun, 2009; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Schreij, Theeuwes, & Olivers, 2010), as it is known that neural representations of attended objects are remapped across saccades (Gottlieb, Kusunoki, & Goldberg, 1998). We measured the allocation of spatial attention at different locations and at different times before and after the saccade by using a probe discrimination task in which participants had to report a Gabor orientation change. Indeed, improvements in probe discrimination can be used as a direct measure of attention allocation (Carrasco, 2011; Deubel & Schneider, 1996; Gersch, Kowler, Schnitzer, & Dosher, 2009; Jonikaitis & Deubel, 2011; Ling & Carrasco, 2006; Neggers et al., 2007). With this novel design we could determine whether spatial attention is predictively remapped before the saccade, and whether, after the saccade, it is allocated to the spatial location of the cue, to the retinotopic location of the cue, or both. By varying the onset of the tilted Gabor test with respect to the saccade, we measured when those attentional benefits appeared or disappeared. In addition to examining the allocation of attention across saccades, we manipulated the status of the attention capturing color cue, either keeping it onscreen after the saccade or removing it during the saccade. This manipulation allowed us to investigate whether the allocation of attention after the saccade depends on the continuing presence of the color cue. If

feature information is used in order to localize attended objects across the saccades, then we should observe a time-dependent effect of the post-saccadic presence of the color cue.

Materials and methods

Participants

Fifteen participants (age between 21 and 29 years, 5 females, normal or corrected-to-normal vision) took part in the experiment (11 participants completed the Transient-cue task, 14 completed the Sustained-cue task, 10 completed both). All except for two of the authors (DJ, MS) were naive as to the purpose of the study. The experiments were undertaken with the understanding and written consent of each subject and were conducted in accordance with the Declaration of Helsinki.

Setup

Participants sat in a quiet and dimly illuminated room. We recorded right-eye gaze position with an SR Research EyeLink 1000 desktop mounted eye-tracker (with a spatial resolution finer than 0.25°, sampling rate of 1000 Hz), calibrated before each new block and whenever necessary. Stimulus presentation and response collection was controlled by an Apple computer and implemented in Matlab (MathWorks, Natick, MA, USA) using Psychophysics and Eyelink toolboxes (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Watson & Pelli, 1983). Stimuli were presented at a viewing distance of 60 cm, on gamma-linearized screens, a 21-inch Sony GDM-F500R (1280 x 1024 pixels, vertical refresh rate of 85 Hz) in Munich, or a 22-inch Compaq P1220 (1024 x 768 pixels, vertical refresh rate of 120 Hz) in Paris.

Main task procedure

Figure 2 depicts the display configuration. During each trial, participants performed two tasks, a saccade task and a probe discrimination task. A trial started with participants fixating a central fixation target forming a "bull's eye" (radius 0.75°) on a gray background (mean luminance 39 cd/m^2). We presented two potential saccade targets – filled black circles (radius 0.75°) – 8º to the left and to the right of the fixation. After a fixation period (mean = 1 s, SD. = 300 ms, cutoff at 3.3 SD.), the fixation target disappeared, and the "bull's-eye" replaced one of the two potential saccade targets. If participants did not make a correct saccade within 700 ms following saccade target appearance, we repeated the trial later during the same experimental session.

In addition, six discrimination-task-related objects (radius 2º) formed two rows composed of three objects each, 6° above and below the fixation and the two saccade target locations. The objects consisted of a stream of flickering stimuli, composed of vertical Gabor patches (frequency: 2.5 cpd; 100% contrast; random phase; standard deviation of Gaussian window: 1.1º; mean luminance 40 cd/m^2) alternating with noise masks (each pixel's gray value from gaussian distribution; M: 0.5; STD: 0.5; cut-off at 0, black, and 1, white; mean luminance 40 cd/m^2), every 24–25 ms (3 frames at 120 Hz refresh rate or 2 frames at 85 Hz refresh rate depending on the setup used). Between 100 ms before and 600 ms after saccade target onset (time selected randomly from a uniform distribution), a probe appeared randomly at one of the six locations, with equal probability. At that location and time, the

Gabor changed orientation for one period of 24–25 ms followed again by a mask. We selected the probe orientation based on a threshold procedure explained below. Once the probe had appeared, no more Gabor patches followed at any of the locations and the noise masks now alternated with blanks. 700 ms after saccade target onset, all objects disappeared and the participant reported the probe orientation (clockwise or counterclockwise from vertical) followed by a response feedback (a beep if incorrect). We stressed that the main task was to make accurate and fast saccades, and told participants not to worry if they did not see the probe.

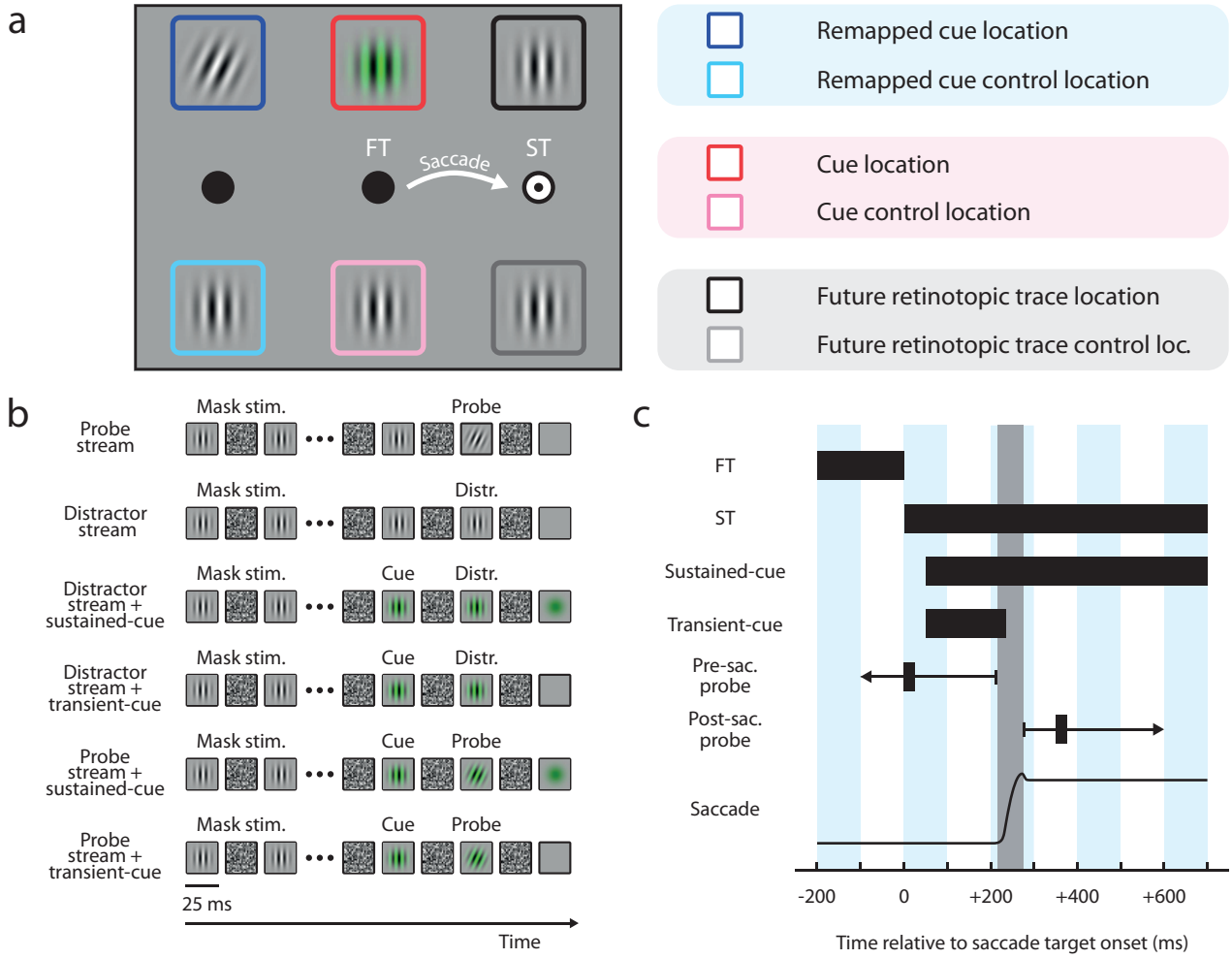


Figure 2. Experimental procedure. (a) *Display setup.* Participants were instructed to shift their gaze to the saccade target (ST), which could appear to the right or to the left of the fixation target (FT). We presented six visual streams composed of alternating Gabor and noise patches above and below FT and ST. Shortly after the onset of ST, an attentional cue (green) appeared directly above or below FT. At different times relative to the saccadic eye movement, a probe (tilted Gabor) appeared within one of the six visual streams and participants reported its orientation. Relative to the position of the cue and to the saccade direction, the probe could appear at the «remapped cue location» (blue frame), the «cue location» (red frame), the «future retinotopic trace location» (black frame) or at their respective control locations mirrored across the horizontal meridian (respective light colors). The schematic is not to scale and the colored frames were not visible during the experiment. (b) *Visual streams.* As a function of the locations of the probe and of the cue, the visual streams could be one of four different streams. The “Distractor stream” was composed of vertical Gabors alternating with noise masks. The “Probe stream” was identical, except that at a random time a tilted Gabor appeared. The “Distractor stream + Sustained-cue”, “Distractor stream + Transient-cue”, “Probe stream + Sustained-cue” and “Probe stream + Transient-cue” streams were similar to the ones described above except that 70 ms after ST onset all Gabors within these streams were green. Note that no Gabors were shown within any streams after the probe presentation, while the green color stayed on only in the Sustained-cue condition. (c) *Stimulus timing.* The FT disappeared first with the onset of the ST, followed 70 ms later by the cue. The saccade started with an average latency of 210 ms. The probe appeared either before the saccade (pre-saccadic probe) or after the saccade (post-saccadic probe). Horizontal arrows denote the time interval during which the probe could appear.

The probe discrimination task served as our measure of attention allocation. We summoned attention by presenting an attention-capturing cue (Carrasco & Yeshurun, 2009; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Schreij et al., 2010), an abrupt color onset stimulus presented above or below central fixation. Specifically, 70 ms after saccade target appearance, the Gaussian envelope covering the cued Gabor patch changed color to green (mean luminance of Gabor + green Gaussian envelope 34 cd/m^2). Participants were asked to ignore this color onset, as the onset location did not predict the location of the probe. In the Transient-cue task, we removed the color cue during the saccade (i.e., the Gabor patch returned to gray); in the Sustained-cue task, the color cue remained onscreen after the saccade, until the end of the trial.

Participants ran a minimum of five one-hour sessions for each of the tasks (if observers performed both tasks, the Sustained-cue condition preceded the Transient-cue condition), each session consisting of at least 480 trials. Before starting the experiment each participant completed a training session (usually taking 15 minutes).

Threshold procedure

Before each session, we evaluated the probe tilt angles that gave matched baseline performance for the probe locations regardless of their eccentricity and presentation time. We used interleaved QUEST staircases (Watson & Pelli, 1983), varying the probe orientation at different locations until participants reached a desired 82% correct discrimination performance. Just like in the main experiment, we asked participants to make a saccade, and 70 ms after the saccade target onset, a cue (abrupt color change) appeared. The cue location could be any of the 6 object locations, but probes appeared always at the cued location. In the threshold procedure, therefore, the cue was 100% valid, instructing participants where to shift attention. We conceived this procedure to ensure that performance was sensitive to attentional modulations, independent of probe timing and of location. Three staircases were evaluated for probes presented 100 ms after the cue onset, corresponding to the pre-saccadic period (about 50 ms before the saccade started). A first staircase was for probes above and below the fixation target (eccentricity 6°, average tilt angle across participants: 17°); a second for the probes above and below the saccade target (eccentricity 10°, tilt ~ 20°); third for the probes presented opposite of the saccade target (eccentricity 10°, tilt ~ 20°). In a different set of trials, we also measured three other staircases for probes presented 450 ms after cue onset, corresponding to the post-saccadic period. Post-saccadic probes had different eccentricities and thus different orientation thresholds (eccentricities 6°, 10º, 17.1º; tilt ~14°, ~20º, ~24º). Only trials in which a correct saccade occurred were used for the threshold procedure. This threshold procedure equated baseline probe discrimination performance even if eccentricity of probes changed across saccades, allowing us to compare probe discrimination across eccentricities as well as before and after the saccade.

Data analysis

We detected saccades offline using an algorithm based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006), computed from subsequent samples in the eye position series. The thresholds for peak velocity and minimum duration used for saccade detection were 3.0 SD and 20

ms, respectively. To create the saccade landing error map (Figure 3b), we used a kernel density estimation based on linear diffusion processes (Botev, Grotowski, & Kroese, 2010).

We discarded trials where the saccade latency was below 100 ms or above 500 ms. We only analyzed trials in which the saccade landed within a 2º radius around its goal. In total we accepted 92% trials: 0.5% of all trials were rejected due to blinks, 7% due to inaccurate saccades and 0.1% due to participants looking at the color onset location.

The performance in the probe discrimination task is expressed as the percentage of correct orientation discriminations. As the probe appeared at a random time, we binned probe presentation times into 100 ms time bins before and after the saccade for further analysis. In pre-saccadic analyses, each bin contained all probes whose presentation ended in a given 100 ms interval; in post-saccadic analyses, each bin contained all probes whose presentation started in a given 100 ms interval. This analysis thus excluded all probes overlapping with the saccade in time. On average for each participant a bin contained around 60 trials. Since there were two response alternatives, the chance level of probe discrimination was at 50%. For the analysis of probe discrimination performance, we pooled data across saccade directions. Statistical analyses included repeated-measure analyses of variance; and direct comparisons between different time bins were done with paired t-tests. Transient-cue and Sustained-cue tasks were compared to each other using a mixed effects ANOVA, which allows for comparisons of conditions containing partly overlapping participant pools.

Results

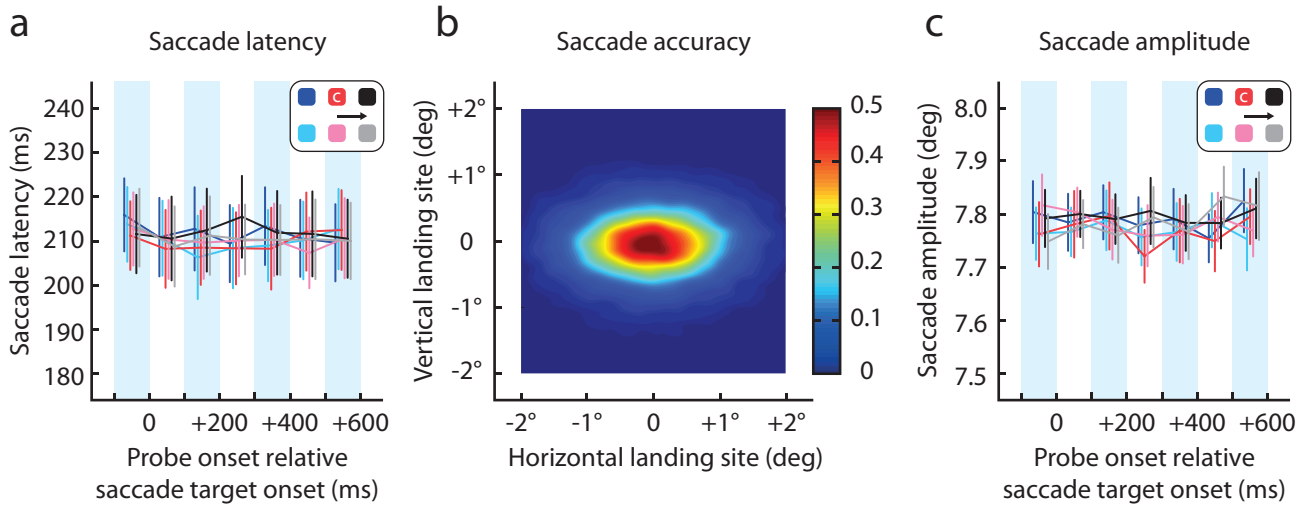


Figure 3. (a) *Saccade latency* as a function of probe presentation time and probe locations. Colors indicate the probe locations with respect to saccade target and onset cue, as described in the small legend icon. Error bars indicate SEM. (b) *Saccade accuracy* for all saccade directions and probe locations. Warmer colors represent higher incidence of saccades to that location. (c) *Saccade amplitude* as a function of probe presentation time and probe location. Same conventions as in panel a. All three panels show data from the Sustained-cue condition. Data from the Transient-cue (not displayed) condition were not statistically different.

The average saccade latency was 210 ± 32 ms (mean ± SEM) in the Sustained-cue task and 228 ± 56 ms in the Transient-cue task. These latencies match those observed in other studies investigating attentional allocation and saccade planning (Deubel & Schneider, 1996; Golomb et al., 2008; Jonikaitis & Deubel, 2011; Rolfs et al., 2011), suggesting that the appearance of the color cue

did not have a major impact on saccade latencies. Additionally, as our display consisted of several flickering stimulus streams, the probe onset itself did not stand out from these background events and so did not disrupt saccade planning. Figure 3a shows that average saccade latencies for probes presented at different locations and at different times after the saccade target onset are largely similar. Repeated measures ANOVAs did not show an effect of either probe position with respect to the saccade target or probe presentation time and this for both tasks (all $p > 0.05$). Figure 3b shows saccade accuracy. Average saccadic errors (as measured in distance from the saccade target center at 8º eccentricity) across participants was 0.23° ± 0.03° in the Sustained-cue task and 0.25° ± 0.05° in the Transient-cue task. Finally, as observed in Figure 3c**,** saccade landing position did not vary as a function of the probe presentation time, or probe position for neither of the tasks (all $p > 0.05$).

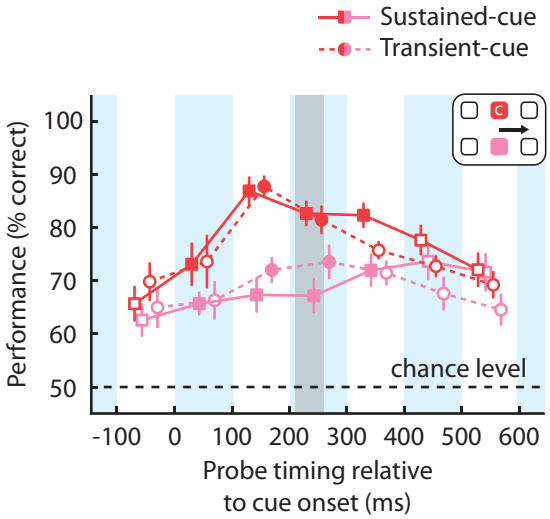


Figure 4. Probe discrimination performance at the cue location before and after the color cue onset for Sustained-cue and Transient-cue conditions. Colors indicate the probe locations as described in the small legend icons. We computed performance in temporal bins separated by 100 ms. For a given temporal bin, filled symbols indicate significant differences between a location of interest and its control, based on repeated-measures t-tests taken separately for the sustained and the transient-cue condition.

Next we analyzed performance in the probe discrimination task. To do so, we computed probe discrimination performance as the percentage of correct discrimination responses for probes appearing within specified 100 ms time bins locked either to the cue onset (Figure 4) or to the saccade onset (Figure 5 and 6). For each trial we defined 3 positions of interest (cue location, remapping & future retinotopic trace) as well their 3 respective controls, mirrored relatively to the saccade vector. We then evaluated the temporal dynamics of attention allocation at these locations, by comparing the actual position with their control for the different time bins. Figure 4 shows probe discrimination performance at the cue location and at its control location for two experimental conditions (for this comparison, we looked at the discrimination performance observed for the 10 participants who did both conditions). For both Sustained-cue and Transient-cue conditions, we observed the typical effect of transient spatial attention, that is discrimination performance improved at the cue location, reaching a maximum around 50-150 ms after the cue onset, and then decreased (Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989).

Next we analyzed discrimination performance over time before and after the saccade, first for the Sustained-cue (see Figure 5) and then for the Transient-cue conditions (see Figure 6). Figure 5b shows that in the Sustained-cue condition, before the saccade began, probe discrimination improved markedly at the cue location with respect to its control location. A repeated-measures ANOVA (with probe time and its location as main factors), showed that probe discrimination performance before saccade onset was affected by time ($F(2,26) = 15.40$; $p < 0.001$), probe location ($F(1,13) = 34.36$ $p < 0.001$) and the interaction between the two factors ($F(2,26) = 12.75$, $p < 0.001$). Probe discrimination performance increased strongly at the cue location as compared to control location for probes presented up to 200 ms before the saccade (200-100 ms before saccade, $t(13) = 2.62$, $p < 0.05$; 100-0 ms before saccade, $t(13) = 9.78$, $p < 0.001$, filled squares in Figure 5b mark statistically significant comparisons).

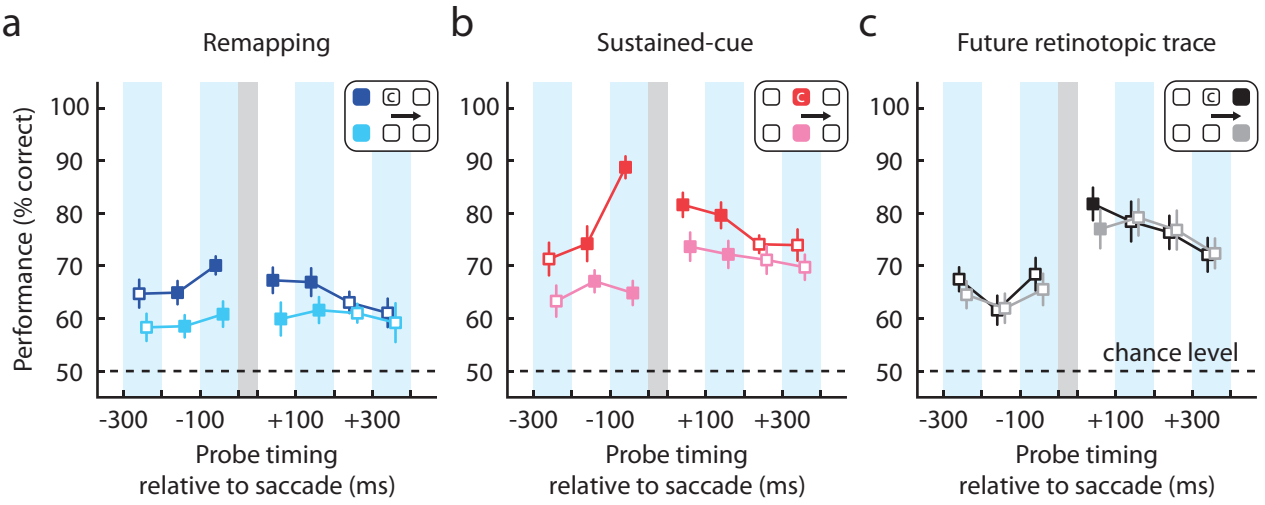


Figure 5. Probe discrimination performance before and after saccades for the Sustained-cue condition. (a) Performance for probes presented at the remapped location and its control, (b), at the cue location and its control, and, (c), at the future retinotopic trace location and its control. Colors indicate the probe locations as described in the small legend icons. We computed performance in temporal bins separated by 100 ms both for probes appearing before the saccade started and for probes appearing after the saccade finished. For a given temporal bin, filled symbols indicate significant differences between a location of interest and its control, based on repeated-measures t-tests.

Figure 5b also shows the discrimination performance for probes presented after the saccade has landed. Probe discrimination performance remained higher at the cued location than at the cue control location after the saccade. Repeated-measures ANOVA showed the main effect of the probe location ($F(1,13) = 11.97$, $p < 0.01$) and an effect of time was approaching significance ($F(3,39) = 2.68$, $p = 0.06$); the interaction was not significant $F(3,39) = 1.33$, $p = 0.27$. Paired t-tests showed that probe discrimination at the cue location was significantly better than that at the control location 0 – 200 ms after the saccade (0-100 ms after saccade, $t(13) = 2.72$, $p < 0.05$; 100-200 ms after saccade, $t(13) = 2.77$, $p < 0.01$). Combined, these results show that the cue improved discrimination performance at its location, and that this benefit is sustained, as a spatiotopic attentional benefit, across the saccade.

Next, we analyzed probe discrimination performance at other locations in the visual field. The first set of locations we analyzed were the locations above and below the saccade target (Figure 2a). Before the saccade starts, these two locations are not directly relevant for the saccade task nor

are they related to the cue location, even though it had been suggested that one of those locations is the location to which predictive remapping is directed (Mathôt & Theeuwes, 2010), a view that is no longer maintained (remapping is directed in the opposite direction see Figure 1a; Krauzlis & Nummela, 2011; Mathôt & Theeuwes, 2011; Rolfs et al., 2011). After the saccade ends, this location on the display now corresponds to the retinotopic trace location for attentional benefits, i.e. the retinal location the cue had previously occupied (Golomb et al., 2008; 2011; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010a; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b). A retinotopic trace exists only after the saccade, thus in the pre-saccadic period we refer to that location as the "future retinotopic trace location". Probe discrimination performance increased at both the future retinotopic trace location and at its control location (Figure 5c**;** effect of time was significant $F(2,26) = 5.54$, $p < 0.01$), but there was no significant difference between the two locations ($F(1,13) = 0.93$, $p = 0.35$), nor an interaction between the two factors ($F(2,26) = 0.44$, $p = 0.65$). Paired t-tests showed no significant differences between the two locations at any time point before the saccade (all $p > 0.05$). Thus, probe discrimination increased at both locations with a similar time course and magnitude, probably due to their proximity to the saccade target (Gersch et al., 2009). This discrimination performance prior to the saccade therefore fails to show the advantage reported by Mathôt and Theeuwes (2010). A possible explanation for this discrepancy, is that Mathôt and Theeuwes stimulus setup created strong apparent motion perception (between pre-saccadic cue and attentional probe), that may have affected their results.

After the saccade, performance at the retinotopic trace location (Golomb et al., 2008) was affected by probe presentation time ($F(3,39) = 3.53$, $p < 0.05$) but not by probe position ($F(1,13) = 0.90$, $p = 0.35$) and probe position did not interact with probe timing ($F(3,39) = 1.28$, $p = 0.29$). T-tests showed that probe discrimination at the retinotopic trace location was better than at its control location ($t(13) = 2.25$, $p < 0.05$) over the interval 0-100 ms after the saccade but not beyond. In other words, there was a short-lived performance advantage at the retinotopic trace location after the saccade in support of earlier reports by Golomb and colleagues (Golomb et al., 2008; 2011; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010a; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b).

Finally, we analyzed the two locations on the other side of the saccade goal. These two locations were related neither to the saccade target nor to the cue, and were in the opposite visual hemifield from the saccade target. However, before the saccade starts, the location at the same vertical position as the cue is the location on the retina that the cue will occupy after the saccade (see Figure 2a) and is therefore the remapped location of the cue (Duhamel et al., 1992; Hall & Colby, 2011; Krauzlis & Nummela, 2011; Kusunoki & Goldberg, 2003; Rolfs et al., 2011). Thus, our pre-saccadic analysis was centered upon finding whether the spatial attention captured by the color cue is predictively remapped to this location before the saccade (Figure 5a), to instantiate the perceptual benefits that we found after the saccade at the same location on the retina (post-saccadic cue location). A repeated-measures ANOVA showed a significant effect of probe position ($F(1,13) = 20.17$, $p < 0.001$); the probe presentation time effect was marginally significant ($F(3,39) = 3.18$, $p = 0.06$); the interaction between the two factors was not significant ($F(3,39) = 0.68$, $p = 0.51$). Paired t-tests revealed that probe discrimination was better at the remapped location than at the control location in time intervals

200-100 ms before saccade onset (t(13) = 3.12, $p < 0.01$) and 100 to 0 ms before saccade onset (t(13) = 5.45, $p < 0.001$).

After the saccade was finished, these two locations on the screen, furthest from the saccade target have no relevance for the effects of either the abrupt onset or the saccade planning. The data show that the post-saccadic probe discrimination was still affected by probe position (F(1,13) = 9.78, $p < 0.01$) but not by probe presentation time (F(3,39) = 1.17, $p = 0.33$), and that there was no interaction (F(3,39) = 0.82, $p > 0.48$). The main effect of probe position was surprising, and turned out unreliable in Transient-cue condition (see bellow).

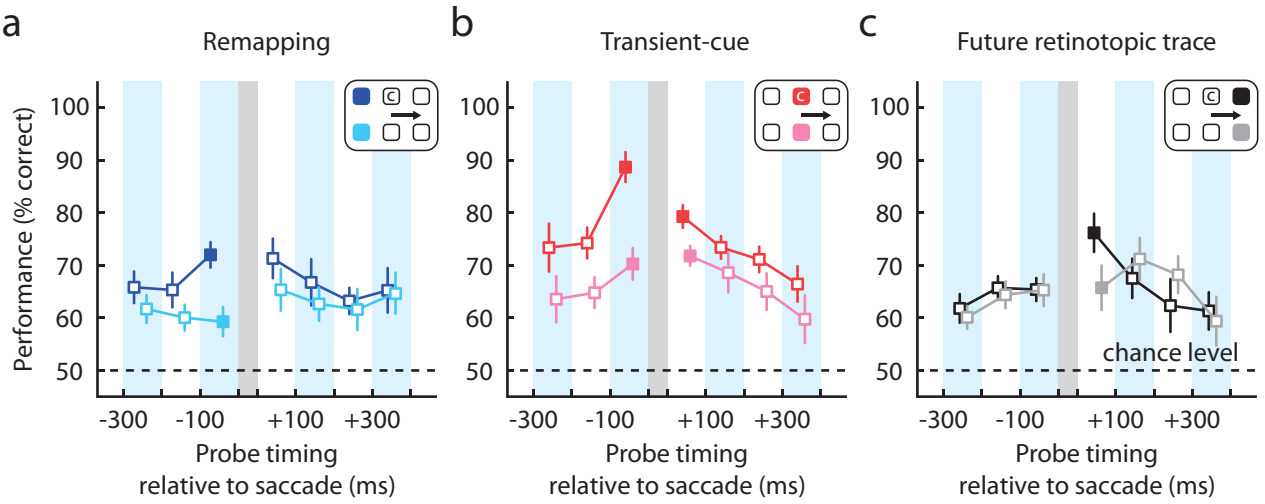


Figure 6. Probe discrimination performance before and after saccades for the Transient cue condition. All conventions are the same as in Figure 5.

Discrimination performance in the Transient-cue condition (Figure 6) where the cue was presented only before the saccade, showed largely similar effects. Discrimination at the cue and cue control locations before the saccade depended on probe presentation time (F(2,20) = 12.37, $p < 0.01$) and probe location (F(1,10) = 15.51, $p < 0.01$), but there was no interaction of these two factors (F(2,20) = 2.36, $p = 0.12$). We obtained the same results after the saccade (probe presentation time, F(3,30) = 12.01, $p < 0.01$; probe position, F(1,10) = 5.18, $p < 0.05$, interaction, F(2,20) = 0.06, $p = 0.97$). Thus, probe discrimination was better at the spatial cue position both, before and after the saccade. In particular, probe discrimination at the cue location was better than at the control location for the first 100 ms after the saccade (t(10) = 2.06, $p < 0.05$). Again, we did not observe any benefits at the future retinotopic trace location before the saccade (probe position, F(1,10) = 0.28, $p = 0.60$; probe time, F(2,20) = 3.22, $p = 0.06$; interaction, F(2,20) = 0.14, $p = 0.86$). As in the Sustained-cue experiment, during the first 100 ms following the saccade, discrimination performance was better at the retinotopic trace location than at the control location (t(10) = 3.36, $p < 0.01$; probe position, F(1,10) = 0.30, $p = 0.59$; probe time, F(3,30) = 8.68, $p < 0.01$; interaction, F(3,30) = 4.37, $p < 0.05$). Thus, in the Transient-cue condition we replicated the attentional retinotopic trace benefits observed in the Sustained-cue condition. Finally, we observed a benefit at the remapped location before the saccade (probe position, F(1,10) = 21.32, $p < 0.001$; time, F(2,20) = 1.05, p=0.36; interaction, F(2,20) = 1.81,

$p = 0.18$), but not after (all ps > 0.05).

To evaluate whether the presence of the color cue after the saccade affected the allocation of spatial attention, we compared Sustained-cue and Transient-cue tasks directly, using mixed effects ANOVA with three factors – probe presentation time, position and task. If cue presence after the saccade had an effect on discrimination benefit at the cue location as compared to the control location, then one would observe an interaction between the three factors. We found no interaction neither between the probe presentation time and position ($F(3,69) = 0.73$, $p = 0.43$), nor an interaction between task, position and time ($F(3,69) = 0.78$, $p = 0.36$). Thus, the presence or absence of an attention capturing cue after the saccade did not affect the attentional benefits at the cue location. This means that feature-based information did not affect discrimination benefits observed at the cue location after the saccade.

Discussion

We investigated the remapping of spatial attention across saccadic eye movements and report the following findings. First, performance at the cue location increased substantially relative to its control, demonstrating the classic attentional benefit of a task-irrelevant onset (see Carrasco, 2011 for a review; Theeuwes, 1994; Yantis & Hillstrom, 1994). Importantly, before the saccade, the discrimination performance also increased at the remapped location of the onset cue, which demonstrates with behavioral measures, the remapping of attention captured by a salient stimulus. This remapping of attention occurred regardless of whether the cue disappeared or stayed onscreen across the saccade. After the saccade, we observed a short-lived improvement in performance at the retinotopic location that the cue occupied before the saccade. This retinotopic trace of attention dissipated within the first 100 ms after the saccade. Moreover, an attentional benefit at the cue location on the screen persisted after the saccade, meaning that transient attention, invoked by an abrupt onset stimulus before saccade, is correctly allocated to its spatiotopic location immediately after the saccade. This effect was evident regardless of the retinal image shift during the saccade and regardless of the fact that the color cue vanished across saccade.

Our findings support neurophysiological studies showing remapping of neural activity. Neural responses to stimuli appearing outside of neurons' visual receptive fields, but at locations that those receptive fields will occupy after the saccade (see Figure 1), have been observed in several areas involved in saccade planning – the frontal eye fields (Sommer & Wurtz, 2006; Umeno & Goldberg, 1997), the lateral intraparietal cortex (Duhamel et al., 1992; Heiser & Colby, 2006; Kusunoki & Goldberg, 2003), and the superior colliculus (Churan, Guitton, & Pack, 2011; Walker, Fitzgibbon, & Goldberg, 1995). Such remapping of visual activity has also been observed in a number of human fMRI (Medendorp et al., 2003; Merriam et al., 2003) and EEG studies (Parks & Corballis, 2008; 2010; Peterburs, Gajda, Hoffmann, Daum, & Bellebaum, 2011). While fMRI studies, due to the sluggishness of signal, demonstrate remapping of memorized stimuli after the saccade (Medendorp et al., 2003; Merriam et al., 2003; 2007), EEG and single cell recording studies demonstrate predictive remapping

of attended stimuli, before the saccades (Duhamel et al., 1992; Kusunoki & Goldberg, 2003; Parks & Corballis, 2008; 2010).

The role of attention in remapping has been discounted frequently (Duhamel et al., 1992; Hall & Colby, 2011; Melcher, 2011; Sommer & Wurtz, 2006). However, our result is in agreement with the established physiology of attention and eye movements. Frontal and parietal areas as well as the superior colliculus, all of which show predictive remapping activity (Duhamel et al., 1992; Kusunoki & Goldberg, 2003; Sommer & Wurtz, 2006; Walker et al., 1995), are also involved in attentional shifts (Bisley & Goldberg, 2003; 2010; Liu, Yttri, & Snyder, 2010; Lovejoy & Krauzlis, 2010; Schall, 2002). Consequently, we argue that it is spatial attention (or attentional pointers) that is (are) remapped across saccade (Cavanagh et al., 2010). Indeed, typically, remapping occurs only attended stimuli (Gottlieb et al., 1998) and both behavioral and neurophysiological studies demonstrate that saccade targets, which are attended as well, are remapped regardless whether participants plan a single saccade (Collins, Rolfs, Deubel, & Cavanagh, 2009; Rolfs et al., 2011), or sequences of saccades (Ostendorf, Liebermann, & Ploner, 2010; Rolfs et al., 2011; Sommer & Wurtz, 2002). Finally, several studies have shown that the location of hand movement targets is also remapped across eye movements (Medendorp & Crawford, 2002; van Pelt & Medendorp, 2008), an expected finding given that planning hand movements to an object leads to the automatic allocation of spatial attention to reach targets (Baldauf & Deubel, 2008; 2010; Jonikaitis & Deubel, 2011; Jonikaitis, Schubert, & Deubel, 2010).

Our study demonstrates both the remapping of spatially cued attention before the saccade and perceptual benefits at the cue's location in the world after the saccade. This lends support to the hypothesis that remapping of visual attention contributes to spatiotopic attention allocation across saccades: even though the object is present in the receptive fields of different visual neurons before and after saccade, the transfer of attention from the cued location to the remapped location before the saccade will bring that attention back to the cue's spatial location once the saccade lands (Cavanagh et al., 2010). Importantly, we observed discrimination benefits for the first 100 ms after the saccade, regardless of whether the color cue was still present in the visual field or not. If perceptual benefits during the first 100 ms after the saccade had occurred contingent on a matching of visual object features across the two fixations, then spatiotopic cueing effects should have been observed only when the cue was visible after the saccade, and not when it was erased. Instead, we observed that removing the color cue during the saccade had little or no effect on attentional benefits at the cue location after the saccade, suggesting that spatiotopic benefits across saccades mainly depend on spatial attention. This result is in line with recent single cell recording studies, showing that after a saccade, visual selectivity to attended features such as color or shape takes around 100 ms to build up in attention modulated visual areas V4 and FEF (Bichot, Rossi, & Desimone, 2005; Zhou & Desimone, 2011). Moreover, recent evidence suggests that FEF neurons detect stimulus changes across saccades (including changes in location, color, or size) a selectivity that also takes some time to develop after the saccade (Crapse & Sommer, 2012). Thus, if the visual system relied only on detecting feature information across saccades, spatiotopic benefits would take more time to occur than observed in single cell recording studies of remapping (Duhamel et al., 1992; Kusunoki & Goldberg, 2003). Spatial attention – rather than visual feature search after the saccade – would prove especially

useful in environments containing many objects sharing similar features. It would be more demanding to find out where relevant features are located before and after the saccade in a crowded environment, rather than just calculating a predicted object position across eye movements. Even though we do not discount that feature-based visual processing could potentially aid in localizing objects in some situations after the saccade, our data demonstrates that predictive remapping of attended targets and spatiotopic attentional allocation after the saccades is the default mode of function in the visual system, even when there are no task demands to update information across saccades, and even when the unique feature of an object is extinguished during the saccade.

Our findings address current controversies concerning the distribution of spatial attention after saccades. Golomb and colleagues have reported that after a saccade, there is a strong attentional benefit at the retinotopic location that had been occupied by a memorized stimulus before the saccade (retinotopic trace location), and that there is only a gradual build-up of attention at the spatial location of the cue (Golomb et al., 2008; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010a; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b). Contrary to our task, those studies used memorized locations to investigate spatiotopic and retinotopic processing benefits after the saccade. The time course of spatial updating across saccades for memorized stimuli might be different, as there is no urgency for the visual system to update information about the stimulus which has long disappeared from the visual field. This is in contrast to the remapping of spatial attention in response to attention grabbing, currently visible stimuli. Future research would need to compare both situations directly.

Our results, combined with those of previous studies, portray a dynamic picture of attention allocation before and after saccadic eye movements. Attention drawn to salient objects before a saccade is remapped around the time the eyes move in the opposite direction of the saccade. As a consequence, attention is continuously allocated to the spatial locations of attended objects in the world across saccades, correcting for the large position shifts that eye movements cause for these objects on the retina and throughout retinotopic cortices. Moreover, the retinal positions of attended pre-saccadic stimuli shows brief attentional benefits after a saccade (Golomb et al., 2008), suggesting that these benefits cannot be immediately extinguished. Combined, such spatial updating of attention may help quickly follow attended targets, despite perpetual eye movements.

Acknowledgments

This research was supported by Chaire d'Excellence Grant to PC, French Ministère de l'Enseignement supérieur et de la Recherche Grant to MS and Deutsche Forschungsgemeinschaft grant JO 980/1-1 to DJ. MR is supported by the 7th Framework Program of the European Union (Marie Curie International Outgoing Fellowship, project number 235625).

Corresponding authors

Correspondence should be addressed to Donatas Jonikaitis (donatas.jonikaitis@psy.lmu.de), Allgemeine und Experimentelle Psychologie, Leopoldstr 13, 80802, Munich, Germany, and Patrick Cavanagh (patrick.cavanagh@parisdescartes.fr), Laboratoire Psychologie de la Perception, Université Paris Descartes, CNRS – UMR 8158, 45, rue des Saints-Pères, Paris, France.

References

Ahw E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, *10*(3), 124–130.

Baldauf, D., & Deubel, H. (2008). Visual attention during the preparation of bimanual movements. *Vision Research*, *48*(4), 549–563.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research*, *50*(11), 999–1013.

Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, *308*(5721), 529–534.

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science*, *299*(5603), 81–86.

Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annual review of neuroscience*, *33*, 1–21.

Botev, Z. I., Grotowski, J. F., & Kroese, D. P. (2010). Kernel density estimation via diffusion. *The Annals of Statistics*, *38*(5), 2916–2957.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial vision*, *10*(4), 433–436.

Carrasco, M. (2011). Visual attention: the past 25 years. *Vision Research*, *51*(13), 1484–1525.

Carrasco, M., & Yeshurun, Y. (2009). Covert attention effects on spatial resolution. *Progress in Brain Research*, *176*, 65–86.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.

Churan, J., Guitton, D., & Pack, C. C. (2011). Context dependence of receptive field remapping in superior colliculus. *Journal of neurophysiology*, *106*(4), 1862–1874.

Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision*, *9*(5), 29.1–9.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior research methods, instruments, & computers : a journal of the Psychonomic Society, Inc*, *34*(4), 613–617.

Crapse, T. B., & Sommer, M. A. (2012). Frontal eye field neurons assess visual stability across saccades. *The Journal of neuroscience*, *32*(8), 2835–2845.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates

space constancy. *Vision Research*, *38*(20), 3147–3159.

Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Research*, *50*(2), 249–259.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*(7), 985–996.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*(5040), 90–92.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(18), 7192–7197.

Gardner, J. L., Merriam, E. P., Movshon, J. A., & Heeger, D. J. (2008). Maps of visual space in human occipital cortex are retinotopic, not spatiotopic. *Journal of Neuroscience*, *28*(15), 3988–3999.

Gersch, T. M., Kowler, E., Schnitzer, B. S., & Dosher, B. A. (2009). Attention during sequences of saccades along marked and memorized paths. *Vision Research*, *49*(10), 1256–1266.

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The native coordinate system of spatial attention is retinotopic. *The Journal of neuroscience*, *28*(42), 10654–10662.

Golomb, J. D., Marino, A. C., Chun, M. M., & Mazer, J. A. (2011). Attention doesn't slide: spatiotopic updating after eye movements instantiates a new, discrete attentional locus. *Attention, Perception and Psychophysics*, *73*(1), 7–14.

Golomb, J. D., Nguyen-Phuc, A. Y., Mazer, J. A., McCarthy, G., & Chun, M. M. (2010a). Attentional facilitation throughout human visual cortex lingers in retinotopic coordinates after eye movements. *The Journal of neuroscience*, *30*(31), 10493–10506.

Golomb, J. D., Pulido, V. Z., Albrecht, A. R., Chun, M. M., & Mazer, J. A. (2010b). Robustness of the retinotopic attentional trace after eye movements. *Journal of Vision*, *10*(3), 19.1–12.

Gottlieb, J., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, *391*(6666), 481–484.

Hall, N. J., & Colby, C. L. (2011). Remapping for visual stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 528–539. doi:10.1098/rstb.2010.0248

Heiser, L. M., & Colby, C. L. (2006). Spatial updating in area LIP is independent of saccade direction. *Journal of neurophysiology*, *95*(5), 2751–2767.

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological science*, *22*(3), 339–347.

Jonikaitis, D., Schubert, T., & Deubel, H. (2010). Preparing coordinated eye and hand movements: dual-task costs are not attentional. *Journal of Vision*, *10*(14), 23. doi:10.1167/10.14.23

Krauzlis, R. J., & Nummela, S. U. (2011). Attention points to the future. *Nature Neuroscience*, *14*(2), 130–131.

Kusunoki, M., & Goldberg, M. E. (2003). The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *Journal of neurophysiology*, *89*(3), 1519–1527.

Ling, S., & Carrasco, M. (2006). When sustained attention impairs perception. *Nature Neuroscience*, *9*(10), 1243–1245.

Liu, Y., Yttri, E. A., & Snyder, L. H. (2010). Intention and attention: different functional roles for LIPd

and LIPv. *Nature Neuroscience*, *13*(4), 495–500.

Lovejoy, L. P., & Krauzlis, R. J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience*, *13*(2), 261–266.

Mathôt, S., & Theeuwes, J. (2010). Evidence for the predictive remapping of visual attention. *Experimental brain research*, *200*(1), 117–122.

Mathôt, S., & Theeuwes, J. (2011). Visual attention and stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 516–527.

Medendorp, W. P. (2011). Spatial constancy mechanisms in motor control. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 476–491.

Medendorp, W. P., & Crawford, J. D. (2002). Visuospatial updating of reaching targets in near and far space. *Neuroreport*, *13*(5), 633–636.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *The Journal of neuroscience*, *23*(15), 6209–6214.

Melcher, D. (2011). Visual stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 468–475.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex. *Neuron*, *39*(2), 361–373.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in human visual cortex. *Journal of neurophysiology*, *97*(2), 1738–1755.

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373.

Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal Of Experimental Psychology-Human Perception And Performance*, *15*(2), 315–330.

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(6), 4026–4031.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*(11), 1631–1647.

Neggers, S. F. W., Huijbers, W., Vrijlandt, C. M., Vlaskamp, B. N. S., Schutter, D. J. L. G., & Kenemans, J. L. (2007). TMS pulses on the frontal eye fields break coupling between visuospatial attention and eye movements. *Journal of neurophysiology*, *98*(5), 2765–2778.

Ostendorf, F., Liebermann, D., & Ploner, C. J. (2010). Human thalamus contributes to perceptual stability across eye movements. *Proceedings of the National Academy of Sciences*, *107*(3), 1229–1234.

Parks, N. A., & Corballis, P. M. (2008). Electrophysiological correlates of presaccadic remapping in humans. *Psychophysiology*, *45*(5), 776–783.

Parks, N. A., & Corballis, P. M. (2010). Human transsaccadic visual processing: presaccadic remapping and postsaccadic updating. *Neuropsychologia*, *48*(12), 3451–3458.

Peterburs, J., Gajda, K., Hoffmann, K.-P., Daum, I., & Bellebaum, C. (2011). Electrophysiological correlates of inter- and intrahemispheric saccade-related updating of visual space. *Behavioural*

Brain Research, *216*(2), 496–504.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*(2), 252–256.

Schall, J. D. (2002). The neural selection and control of saccades by the frontal eye field. *Philosophical transactions of the Royal Society of London Series B, Biological sciences*, *357*(1424), 1073–1082.

Schall, J. D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research*, *44*(12), 1453–1467.

Schreij, D., Theeuwes, J., & Olivers, C. N. L. (2010). Irrelevant onsets cause inhibition of return regardless of attentional set. *Attention, Perception and Psychophysics*, *72*(7), 1725–1729.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*(5212), 889–893.

Sommer, M. A., & Wurtz, R. H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, *296*(5572), 1480–1482.

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*(7117), 374–377. doi:10.1038/nature05279

Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision*, *11*(2).

Theeuwes, J. (1994). Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *Journal Of Experimental Psychology-Human Perception And Performance*, *20*(4), 799–806.

Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of neurophysiology*, *78*(3), 1373–1383.

van Pelt, S., & Medendorp, W. P. (2008). Updating target distance across eye movements in depth. *Journal of neurophysiology*, *99*(5), 2281–2290.

Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of neurophysiology*, *73*(5), 1988–2003.

Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

Yantis, S., & Hillstrom, A. P. (1994). Stimulus-driven attentional capture: evidence from equiluminant visual objects. *Journal Of Experimental Psychology-Human Perception And Performance*, *20*(1), 95–107.

Zhou, H., & Desimone, R. (2011). Feature-based attention in the frontal eye field and area V4 during visual search. *Neuron*, *70*(6), 1205–1217.

5. General discussion

In this last section, we will review the main issues addressed in this thesis and examined in studies that were presented. We will then briefly discuss each study by summarizing their main results and interpretations. Finally we will suggest subsequent experiments to extend our findings and either confirm or reject the conclusions we have drawn.

5.1 Main issues of the thesis

The central purpose of this thesis was to test with simple behavioral methods a mechanism that contributes to space constancy that has recently emerged from electrophysiology evidence: remapping. We have linked this mechanism to the psychophysical literature of trans-saccadic perception and, in particular, we have demonstrated that its characteristics can be evaluate through the investigation of attentional benefits and location judgments across eyes and head movements.

Therefore, we first examined whether the spatial location of attended targets can be recovered despite changes in retinal coordinates. To do so we used the compelling perceptual phenomenon of apparent motion to judge the displacement between two probes, one presented before and the other after an eye movement. After establishing that apparent motion was seen in spatiotopic coordinates, we measured different aspects of that recovery of spatial location across saccades. Then, the accuracy across several locations in the visual field allowed us to specify that the observed correction errors rely on local as opposed to global mechanisms of correction.

Next we demonstrated that the temporal dynamics of the saccadic correction (that we attribute to remapping) could be directly visualized in the perceived motion path of a salient object that was moving continuously while a saccade was executed across its trajectory. This method allowed us to examine the link between peri-saccadic mislocalization effects and the correction of perceived location for saccades. Finally, our trans-saccadic apparent motion procedure was used to assess whether corrections for saccades on retinotopic maps could possibly deal with extra-retinal locations.

The results from these studies were used to compare our model of space constancy against those of others described in the literature. The last study of this thesis tested the predictions of the model for the allocation of attention to different positions of interest both before and after a saccade.

Finally, it is not only our eye movements that change the projections on our retinas, movements of the head do so as well, and quite often the eyes and head move together to orient the gaze to different targets. However, we do not experience an unstable world when our head moves. Thus we decided to extend our model to head movements. As we had done for saccades, we determined the accuracy of the correction of location for different types of head movements using a displacement judgment, and compared our results to previous reports of accurate correction for head movements.

Altogether these studies examined aspects of our model of space constancy as well as more general aspects of the mechanism of remapping. Across these studies, we tried to link psychophysical and electrophysiological evidence in a single framework and help bring a better understanding of the space constancy problem and the mechanisms that achieve it.

5.2 Review of the main results and interpretations

5.2.1. Spatiotopic apparent motion reveals local variations in space constancy

In the first study of this thesis, we showed that remapping could be evaluated in a non-invasive fashion using an apparent motion procedure. We found, as reported previously by Rock and Ebenholtz (1962), that apparent motion was seen in spatial rather than retinal coordinates suggesting that location of the pre-saccadic probe has been corrected for the effects of the intervening saccade. We evaluated the accuracy of this correction — remapping — at different positions in the visual field and for different directions of saccade. We found that the accuracy of correction varied across locations and so could only be explained by a local mechanism such as physiological "remapping" of attention pointers. The variability of the correction argued against global mechanisms that would predict a constant correction for the entire visual field (and therefore a similar error at all locations) such as the shift and subtract correction (Sperry, 1950; von Holst & Mittelstaedt, 1950), the saccade landscape theory and its variants (Bridgeman et al., 1994; Deubel et al., 2002), and spatiotopic maps (e.g. Andersen et al., 1985; Bischof & Kramer, 1968; Breitmeyer et al., 1982). The errors of correction that we found were also sustained rather than transient and so we suggested that they reflect the final, stable saccadic correction. These stable errors are unlike the large, dynamic mislocalizations reported for very brief stimuli presented around the time of a saccade (Matin & Pearce, 1965; Ross et al., 1997).

This first study demonstrated the advantages of using apparent motion to study trans-saccadic perception.

5.2.2. Temporal dynamics of remapping captured by peri-saccadic continuous motion

In the second study of this thesis, we devised a continuous motion stimulus that allowed us to directly visualize trans-saccadic corrections as they happen. We used a salient attended probe moving on a linear path before, during and after the saccade so that the perceived motion path would capture the dynamics of remapping. We found that the continuous motion trace was seen as two misaligned but linear segments, with the pre-saccadic segment shifted in the direction opposite to the saccade. We explain this result by suggesting that the trajectory was corrected for the effect of the saccade and perceived in roughly spatiotopic rather than retinotopic coordinates with however a systematic overestimation of the saccade amplitude leading to errors of remapping.

Interestingly, none of the mislocalization effects reported for brief individual probes were seen in the motion trace. The moving dot was seen not to jump in the direction of saccade just prior to the saccade and then back to the spatial path after the saccade as would be expect from the peri-saccadic compression results (Ross et al., 1997) nor was it seen to follow a three-part curve as expected from peri-saccadic mislocalization (Honda, 1989; Matin & Pearce, 1965). Both pre- and post-saccadic segments appeared to be linear, with nevertheless and offset between them.

We next measure the timing of the break between the two segments by introducing a second physical shift. This procedure allowed us to see that remapping compensation was in place when the saccade landed, a result in agreement with the observed dynamics of physiological remapping

(Kusunoki & Goldberg, 2003; Nakamura & Colby, 2002). Finally, the difference between our results and the pre-saccadic mislocalizations findings (Honda, 1989; Matin & Pearce, 1965; Ross et al., 1997) suggested that the pre-existing position information of the motion probe outweighed the mislocalization effects that would be seen with individual, flashed probes.

5.2.3. Visual spatial constancy for head roll and head translation

In the third study of this thesis we evaluated the accuracy of the correction of location for the movement of the head. As head movements last systematically longer than saccades we could not use our trans-saccadic apparent motion procedure (Caelli & Finlay, 1979) so we developed a closely related task. Specifically, by using slightly longer delay between the pre- and post-movement probes, we were able to ask observers to report the perceived direction of displacement between the two probes rather than perceived motion direction. Base on these reports of perceived direction, we evaluated the compensations of pre-movement location occurring for head roll and head translation. Previous literature had shown that these two types of head movement were corrected with high accuracy. We found that the displacements between probes were again seen more in spatiotopic than retinotopic coordinates. There were, however, significant errors for head roll, but not for head translation. We suggest that the disparity compared to previous reports comes from differences in our procedures. Previous studies allowed a long delay of up to 2 seconds before an action was made toward the remembered location of the pre-movement probe. This might allow time for the contribution of later arriving signals indicating head position. In contrast, our rapid, perceptual judgments might rely only on earlier signals and these could have different time constants for the different vestibular sources.

5.2.4. Apparent motion from outside the visual field, retinotopic cortices may register extra-retinal positions

In the fourth study of this thesis, we looked at the fate of a target representation when the correction of location for the effects of the eye movement – remapping – specifies a location outside the visual field. This specific condition happens when a saccade is made away from an attended target near the edge of the visual field. We first report that apparent motion can be experienced between two attended dots presented at two different locations in space but stimulating, across a saccade, grossly the same location at the edge of the visual field. Moreover, apparent motion was still reported in the condition where the first location is brought outside the visual field by the displacement of the eye.

This study thus implies that our model of shifting attention pointers, driven by remapping, should consider the fact that the visuo-motor maps where remapping occurs also represent extra-retinal locations.

5.2.5. Allocation of attention across saccade

In the last study of this thesis we directly tracked the allocation of attention both before and after the saccade. Specifically, we were interested in the dynamic allocation of attention at three positions of interest for remapping, both before and after the saccade. These are: the position of the pre-saccadic, attention-drawing cue (attended location); the position offset from the cue in the direction of the saccade (future retinotopic trace location) and the location offset from the cue in the direction opposite to the saccade (remapped location), that is, the post-saccadic retinal position of the cue. We found the expected rise in performance at the attended location that is also present after the saccade without the temporary loss that would arise if the visual system had to locate the cue anew.

We attribute that spatiotopic benefit across the saccade to a remapping of attention preceding the saccade, an effect that we indeed observe at the position offset from the cue in the opposite direction of saccade. We also observe after saccade, the previously reported retinotopic trace of attention (Golomb et al., 2008) to the position offset of the cue in the direction of the saccade. No attentional benefit could however be found at that same position before saccade, suggesting that remapping indeed goes in the opposite direction of the saccade.

These results then strongly support our model of space constancy based on a transfer of attention pointers preceding the eye movement (Cavanagh et al., 2010) and especially show that attentional benefits at the cue location after the saccade depend on pre-saccadic activation of the remapped location, benefits that are then shifted into alignment with the cue location by the eye movement.

5.3 Perspectives: Attention transfer for space constancy

In this thesis, we have shown that target locations are corrected for the effect of eyes and head movements with a fair degree of accuracy. These corrections of location allow us to see apparent motion as well as probe displacement across eye and head movements in a spatiotopic rather than a retinotopic reference frame. From the spatial accuracy of the corrections evaluated for different locations across the visual field we conclude that the mechanism necessary to compensate eyes and head movement was most likely to be a local correction, similar to or mediated by physiological remapping reported in visuo-motor centers (Duhamel et al., 1992). We then determined the spatial as well as temporal characteristics of remapping and found that it could operate on targets outside the visual field. Across our experiments we demonstrated a link between remapping and the recovery of perceived target location across eye and head movements.

In our last experiment, we demonstrated that the attention captured by a transient visual cue is remapped, even before the saccade, to the retinal location the cue will have following the saccade. This remapping allowed sustained attentional benefits at the spatial location of the attention cue and thus suggested that the remapping of attention is a behavioral correlate of physiological remapping. We therefore demonstrated a second link between remapping and attention.

Given our evidence for these two links, it is clear that there is a remaining double-link between location updating, remapping, and attention that is untested. Attention certainly plays a role in the performance we measured. First, our experiments required attention simply to perform the tasks and second, apparent motion, our measure in several studies, has been frequently suggested to be mediated by attention (e.g. Cavanagh & Mather, 1989; Dick et al., 1991; Verstraten et al., 2000). However, we have not yet directly verified a causal role for attention in our spatiotopic report of motion and probe displacement. This link would be required if shifting attentional pointers were the mechanism underlying the correction of perceived location for the effects of eyes and head movement.

Further work is then required to fully test our model of space constancy based on a remapping of attention pointers. The next section will address three possible directions for continued research. The first proposition will deal with the missing link between remapping of attention pointers and space constancy by considering whether space constancy is found for the whole visual scene or only for attended locations, we will considerate as well as the missing double-link between location updating, attention and remapping. The second proposition will question the link between target location and the properties of the target. In particular, we will propose further studies on the nature of visual integration across saccades in order to determine whether pre-saccadic attention is actually deployed in the direction opposite that of the saccade. Then a last proposition will deal with the observed inaccuracy of space constancy for head roll.

First, the link between remapping of activity on the saccade (attention) maps and space constancy can be addressed by disabling the remapping process. For example, transcranial magnetic stimulation over the saccade areas such as the frontal eye fields or the intraparietal sulcus is known to affect spatial updating of location across saccades (Morris, Chambers, & Mattingley, 2007; Ostendorf, Kilias, & Ploner, 2011) as well as the coupling of spatial attention and the saccade target (Neggers et al., 2007). But will it make the perception for the world also appears less stable across free eye movements in a natural setting? Will observers see the entire visual scene as shifting (uncorrected) as we do when we push our eye ball? Rather than seeing the entire scene move with each saccade, subjects might see only the target moving (uncorrected) with an otherwise stable background.

Indeed if the background stays steady it will mean, as suggested by the remapping hypothesis, that the attended targets are remapped and the rest of the visual field is acquired anew and assumed to be stable. On the other hand, if everything appears to move with each saccade, it will suggests that a global correction is occurring based on the remapping vector, one that is applied to all items, attended or not. The outcome of this research would allow us to decide among possible models of space constancy.

Moreover, if it is indeed possible to disturb activity in visuo-motor areas, such as the frontal eye fields, then will it lead to the absence of the remapped attentional benefits in the opposite direction of the saccade? And if it is the case, will it have an incidence on the updating of location across saccade? We propose here to combine in a single experiment of TMS perturbation, both measures of attentional benefits and of location judgment. We expect that TMS pulses over FEF might eliminate

the deployment of attentional pointers, leading therefore on drastic perturbation of location updating. Such experiment will then test the ultimate double-link between location updating, attention and remapping.

Second, as demonstrated in our last study, every time our eyes move, the attention currently allocated to a target is predictively deployed in the opposite direction of the saccade to be ready at the expected new retinal location of a target. Then, it will be interesting to see whether feature information can be accumulated from various retinal locations, if they are all locations of the same attended object before and after eye or head movement. Indeed, the visual system has acquired the ability to integrate information from targets across multiple locations in space and time (e.g. Cavanagh, Holcombe, & Chou, 2008; di Lollo, 1980). However, one of the more challenging conditions for integration occurs across each eye movement when visual features that are sampled at different locations before and after the saccade must be combined.

These future studies should therefore examine aspects of integration, using for example the specific case of target motion presented both before and after a saccade. Previous papers show that motion signals from biological stimuli (Verfaillie et al., 1994) as well as simple patches of dots in motion (Melcher & Morrone, 2003) could be integrated across saccades. In these studies, two motion signals were presented at the same position in space, first before and then after a saccade. Participants were able to integrate the two signals together, better reporting the direction of an ambiguous motion stimulus. These results showed the ability of the visual system to integrate information in space, combining signals stimulating different locations on the retina as long as they correspond to the same location in space.

In contrast to Melcher and Morrone (2003) study, we suggest here to look at whether two motion signals at two different locations in space, both of them presented just before the saccade, could be integrated if the first position corresponds to an attended target while a second corresponds to its remapped position (opposite direction of saccade, that is the location the target will have after a saccade). We showed in this thesis that attention takes samples both from the pre-saccadic target location and from its expected post-saccadic location (remapped location) before the beginning of the saccade. We therefore could expect to find an integration of the two signals across both space and time. This effect could be a benefit (increase of performance) when the two signals are consistent (same direction) or a cost if they are different. This effect, if it exists, has implications for interference with attention in critical situations if, for any reason, some irrelevant stimulus falls in the remapped location of target of interest just before an eye movement. It could then be important to develop interference-avoidance algorithms to prevent irrelevant targets from appearing at remapped locations.

Finally, the last perspective for future research emerges from our results collected in the head movement experiment. The systematic errors found with head roll will allow us to test the different factors that correct the shifts in retinal projections that occur across head movements. We suggested that efference copy was an important source of correction because it is available before the others (optic flow, proprioception, vestibular input). To test its role for our rapid perceptual displacement judgment, we would compare updating for active versus passive head movement where efference

copy is only available for the active movement. Then optic flow could be systematically tested by comparing updating in light and dark visual environments. The role of vestibular signals in head roll could be evaluated in a comparison between supine and upright positions. It has been shown that head roll compensations reported with delayed action are perturbed by the absence gravity cues from the otoliths in a supine position (Klier et al., 2005). It will then be interesting to see whether this vestibular information is important for our perceptual tests of head movement updating. Finally proprioception might be tested either by using anesthesia of the neck muscles (in a passive head roll movement) or using updating judgment at different times relatively to the head movement, indeed during the movement accurate proprioceptive feedbacks should not yet be available. The results of these tests will help determine the source of the inaccuracy in correction for head roll that we found.

The different experiments presented in this thesis clearly demonstrate that location judgments and attentional benefits allow us to evaluate the role of remapping in space constancy. As described in the introduction, several simple or complex solutions have been proposed to explain space constancy. We propose that space constancy is mediate through the remapping of attention pointers allowing the recovery of target location and repositioning of attentional benefits across eyes, head, or body movements.

6. Bibliography

Afraz, S.-R., & Cavanagh, P. (2008). Retinotopy of the face aftereffect. *Vision Research*, *48*(1), 42–54.

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, *230*(4724), 456–458.

Andersen, R. A., & Mountcastle, V. B. (1983). The influence of the angle of gaze upon the excitability of the light- sensitive neurons of the posterior parietal cortex. *The Journal of Neuroscience*, *3*(3), 532 –548.

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal Representation of Space in the Posterior Parietal Cortex and Its Use in Planning Movements. *Annual Review of Neuroscience*, *20*(1), 303–330.

Awater, H., & Lappe, M. (2006). Mislocalization of Perceived Saccade Target Position Induced by Perisaccadic Visual Stimulation. *The Journal of Neuroscience*, *26*(1), 12 –20.

Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, *10*(3), 124–130.

Barlow, H. B. (1953). Summation and inhibition in the frog's retina. *The Journal of Physiology*, *119*(1), 69 –88.

Bell, C. (1981). An efference copy which is modified by reafferent input. *Science*, *214*(4519), 450 –453.

Bellebaum, C., & Daum, I. (2006). Time course of cross-hemispheric spatial updating in the human parietal cortex. *Behavioural Brain Research*, *169*(1), 150–161.

Bellebaum, C., Hoffmann, K.-P., & Daum, I. (2005). Post-saccadic updating of visual space in the posterior parietal cortex in humans. *Behavioural Brain Research*, *163*(2), 194–203.

Ben Hamed, S., Duhamel, J.-R., Bremmer, F., & Graf, W. (2001). Representation of the visual field in the lateral intraparietal area of macaque monkeys: a quantitative receptive field analysis. *Experimental Brain Research*, *140*(2), 127–144.

Berman, R. A., & Colby, C. (2009). Attention and active vision. *Vision Research*, *49*(10), 1233–1248.

Berman, R. A., & Wurtz, R. H. (2010). Functional Identification of a Pulvinar Path from Superior Colliculus to Cortical Area MT. *The Journal of Neuroscience*, *30*(18), 6342 –6354.

Berthoz, A., Israël, I., Georges-Francois, P., Grasso, R., & Tsuzuku, T. (1995). Spatial memory of body linear displacement: what is being stored? *Science*, *269*(5220), 95 –98.

Bischof, N., & Kramer, E. (1968). Untersuchungen und Überlegungen zur Richtungswahrnehmung bei willkürlichen sakkadischen Augenbewegungen. *Psychological Research*, *32*(3), 185–218.

Bloomberg, J., Jones, G. M., & Segal, B. (1991). Adaptive modification of vestibularly perceived rotation. *Experimental Brain Research*, *84*(1), 47–56.

Blouin, J., Gauthier, G., van Donkelaar, P., & Vercher, J.-L. (1995). Encoding the position of a flashed visual target after passive body rotations. *Neuroreport*, *6*, 1165–1168.

Blouin, J., Labrousse, L., Simoneau, M., Vercher, J.-L., & Gauthier, G. M. (1998). Updating visual space during passive and voluntary head-in-space movements. *Experimental Brain Research*, *122*(1), 93–100.

Bockisch, C. J., & Miller, J. M. (1999). Different motor systems use similar damped extraretinal eye position information. *Vision Research*, *39*(5), 1025–1038.

Breitmeyer, B. G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. *Acta Psychologica*, *52*(3), 175–196.

Brenner, E., & van den Berg, A. V. (1996). The Special Role of Distant Structures in Perceived Object Velocity. *Vision Research*, *36*(23), 3805–3814.

Bridgeman, B. (2007). Efference copy and its limitations. *Computers in Biology and Medicine*, *37*(7), 924–929.

Bridgeman, B. (2010). How the brain makes the world appear stable, *1*(2), 69–72.

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*(6), 719–722.

Bridgeman, B., & Stark, L. (1991). Occular proprioception and efference copy in registerung visual direction. *Vision Research*, *31*(11), 1903–1913.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A Theory of Visual Stability Across Saccadic Eye Movements. *Behavioral and Brain Sciences*, *17*(02), 247–258.

Burr, D. C., Holt, J., Johnstone, J. R., & Ross, J. (1982). Selective depression of motion sensitivity during saccades. *The Journal of Physiology*, *333*(1), 1 –15.

Burr, D. C., & Morrone, M. C. (2011). Spatiotopic coding and remapping in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 504–515.

Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, *371*(6497), 511–513.

Caelli, T., & Finlay, D. (1979). Frequency, phase, and colour coding in apparent motion. *Perception*, *8*(1), 59–68.

Carlson-Radvansky, L. A. (1999). Memory for relational information across eye movements. *Perception & Psychophysics*, *61*(5), 919–934.

Carlson-Radvansky, L. A., & Irwin, D. E. (1995). Memory for structural information across eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*(6), 1441–1458.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525.

Castet, E., Jeanjean, S., & Masson, G. S. (2002). Motion perception of saccade-induced retinal translation. *Proceedings of the National Academy of Sciences*, *99*(23), 15159 –15163.

Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. *Nature Neuroscience*, *3*(2), 177–183.

Cavanagh, P., Holcombe, A. O., & Chou, W. (2008). Mobile computation: Spatiotemporal integration of the properties of objects in motion. *Journal of Vision*, *8*(12).

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*(4), 147–153.

Cavanagh, P., & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*(2), 103–129.

Cavanaugh, J., & Wurtz, R. H. (2004). Subcortical Modulation of Attention Counters Change Blindness. *The Journal of Neuroscience*, *24*(50), 11236–11243.

Colby, C. L., Duhamel, J. R., & Goldberg, M. E. (1996). Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *Journal of Neurophysiology*, *76*(5), 2841 –2852.

Cullen, K. E. (2012). The vestibular system: multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences*, *35*(3), 185–196.

Currie, C. B., McConkie, G. W., Carlson-Radvansky, L. A., & Irwin, D. E. (2000). The role of the saccade target object in the perception of a visually stable world. *Perception & Psychophysics*, *62*(4), 673–683.

Daniel, P. M., & Whitteridge, D. (1961). The representation of the visual filed on the cerebral cortex in monkeys. *The Journal of Physiology*, *159*, 203–221.

Dassonville, P., Schlag, J., & Schlag-Rey, M. (1992). Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Visual Neuroscience*, *9*(3-4), 261–269.

Dassonville, P., Schlag, J., & Schlag-Rey, M. (1995). The use of egocentric and exocentric location cues in saccadic programming. *Vision Research*, *35*(15), 2191–2199.

Deubel, H. (2004). Localization of targets across saccades: Role of landmark objects. *Visual Cognition*, *11*(2/3), 173–202.

Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research*, *38*(20), 3147–3159.

Deubel, H., Elsner, T., & Hauske, G. (1987). Saccadic eye movements and the detection of fast-moving gratings. *Biological Cybernetics*, *57*(1), 37–45.

Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across saccades and during fixation. *Vision Research*, *50*(2), 249–259.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837.

Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*(7), 985–996.

Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *The Brain's eye: Neurobiological and clinical aspects of oculomotor research* (Vol. Volume 140, pp. 165–180). Elsevier.

di Lollo, V. (1980). Temporal integration in visual memory. *Journal of Experimental Psychology: General*, *109*(1), 75–97.

Dick, M., Ullman, S., & Sagi, D. (1991). Short- and long-range processes in structure-from-motion. *Vision Research*, *31*(11), 2025–2028.

Duhamel, Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*(5040), 90–92.

Duhamel, J.-R., Bremmer, F., BenHamed, S., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, *389*(6653), 845–848.

Ezzati, A., Golzar, A., & Afraz, A. S. R. (2008). Topography of the motion aftereffect with and without eye movements. *Journal of Vision*, *8*(14).

Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision: the psychology of looking and seeing*. New York, NY, US: Oxford University Press.

Fischer, B., Boch, R., & Bach, M. (1981). Stimulus versus eye movements: Comparison of neural activity in the striate and prelunate visual cortex (A17 and A19) of trained rhesus monkey. *Experimental Brain Research*, *43*(1), 69–77.

Fracasso, A., Caramazza, A., & Melcher, D. (2010). Continuous perception of motion and shape across saccadic eye movements. *Journal of Vision*, *10*(13), 1–17.

Galletti, C., & Battaglini, P. P. (1989). Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *The Journal of Neuroscience*, *9*(4), 1112–1125.

Galletti, C., Battaglini, P. P., & Fattori, P. (1995). Eye Position Influence on the Parieto-occipital Area PO (V6) of the Macaque Monkey. *European Journal of Neuroscience*, *7*(12), 2486–2501.

Gardner, J. L., Merriam, E. P., Movshon, J. A., & Heeger, D. J. (2008). Maps of Visual Space in Human Occipital Cortex Are Retinotopic, Not Spatiotopic. *The Journal of Neuroscience*, *28*(15), 3988 –3999.

Gauthier, G. M., Nommay, D., & Vercher, J.-L. (1990). Ocular muscle proprioception and visual localization of targets in man. *Brain*, *113*(6), 1857 –1871.

Gibson, J. J. (1950). *The perception of the visual world.* Oxford, England: Houghton Mifflin.

Gibson, J. J. (1966). *The senses considered as perceptual systems*. Oxford, England: Houghton Mifflin.

Glasauer, S., & Brandt, T. (2007). Non-commutative updating of perceived self-orientation in three dimensions. *Journal of Neurophysiology*.

Gnadt, J., & Andersen, R. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Experimental Brain Research*, *70*(1), 216–220.

Goldberg, M. E., Bisley, J. W., Powell, K. D., & Gottlieb, J. P. (2006). Chapter 10 Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Visual Perception Fundamentals of Awareness: Multi-Sensory Integration and High-Order Perception* (Vol. Volume 155, Part B, pp. 157–175). Elsevier.

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, *64*(2), 489–508.

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The Native Coordinate System of Spatial Attention Is Retinotopic. *The Journal of Neuroscience*, *28*(42), 10654–10662.

Gottlieb, J. P. (2007). From Thought to Action: The Parietal Cortex as a Bridge between Perception, Action, and Cognition. *Neuron*, *53*(1), 9–16.

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, *391*(6666), 481–484.

Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In K. Akins (Ed.), *Perception Vancouver Studies in Cognitive Science* (Oxford University Press., pp. 89–110). England.

Grüsser, O.-J., Krizic, A., & Weiss, L.-R. (1987). Afterimage movement during saccades in the dark. *Vision Research*, *27*(2), 215–226.

Guthrie, B. L., Porter, J. D., & Sparks, D. L. (1983). Corollary discharge provides accurate eye position to the oculomotor system. *Science*, *221*, 1193–1195.

Hall, N. J., & Colby, C. L. (2011). Remapping for visual stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 528–539.

Hallett, P. E., & Lightstone, A. D. (1976a). Saccadic eye movements towards stimuli triggered by prior saccades. *Vision Research*, *16*(1), 99–106.

Hallett, P. E., & Lightstone, A. D. (1976b). Saccadic eye movements to flashed targets. *Vision Research*, *16*(1), 107–114.

Hamker, F. H., Zirnsak, M., Calow, D., & Lappe, M. (2008). The Peri-Saccadic Perception of Objects and Space. *PLoS Comput Biol*, *4*(2), e31.

Harrington, D. O. (1981). *The Visual Fields: A Textbook and Atlas of Clinical Perimetry*. St. Louis, MO: Mosby.

Hass, C. A., & Horwitz, G. D. (2011). Effects of microsaccades on contrast detection and V1 responses in macaques. *Journal of Vision*, *11*(3).

Heiser, L., M., & Colby, C., L. (2006). Spatial updating in area LIP is independent of saccade direction. *Journal of Neurophysiology*, *95*, 2751–2767.

Henderson, J. M., & Hollingworth, A. (1999). The role of fixation position in detecting scene changes across saccades. *Psychological Science*, *10*(5), 438.

Hershberger, W. (1987). Saccadic eye movements and the perception of visual direction. *Attention, Perception, & Psychophysics*, *41*(1), 35–44.

Hirsch, J., & Curcio, C. A. (1989). The spatial resolution capacity of human foveal retina. *Vision Research*, *29*(9), 1095–1101.

Hoffman, J., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Attention, Perception, & Psychophysics*, *57*(6), 787–795.

Honda, H. (1985). Spatial localization in saccade and pursuit-eye-movement conditions: A comparison of perceptual and motor measures. *Perception & Psychophysics*, *38*(1), 41–46.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception & Psychophysics*, *45*(2), 162–174.

Honda, H. (1991). The time courses of visual mislocalization and of extraretinal eye position signals at the time of vertical saccades. *Vision Research*, *31*(11), 1915–1921.

Honda, H. (1993). Saccade-contingent displacement of the apparent position of visual stimuli flashed on a dimly illuminated structured background. *Vision Research*, *33*(5–6), 709–716.

Honda, H. (2006). Achievement of transsaccadic visual stability using presaccadic and postsaccadic visual information. *Vision Research*, *46*(20), 3483–3493.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of Physiology*, *160*(1), 106 –154.

Ibbotson, M. R., Price, N. S. C., Crowder, N. A., Ono, S., & Mustari, M. J. (2007). Enhanced Motion Sensitivity Follows Saccadic Suppression in the Superior Temporal Sulcus of the Macaque Cortex. *Cerebral Cortex*, *17*(5), 1129–1138.

Ilg, U. J., Bridgeman, B., & Hoffmann, K. P. (1989). Influence of mechanical disturbance on oculomotor behavior. *Vision Research*, *29*(5), 545–551.

Irwin, D. E. (1992). Perceiving an integrated visual world. In D. E. Meyer & S. Kornblum (Eds.), *Attention and performances XIX* (pp. 121–142). Cambridge, MA: MIT Press.

Israël, I., & Berthoz, A. (1989). Contribution of the otoliths to the calculation of linear displacement. *Journal of Neurophysiology*, *62*(1), 247 –263.

Israël, I., Ventre-Dominey, J., & Denise, P. (1999). Vestibular information contributes to update retinotopic maps. *NeuroReport*, *10*(17).

Jeffries, S. M., Kusunoki, M., Bisley, J. W., Cohen, I. S., & Goldberg, M. E. (2007). Rhesus monkeys mislocalize saccade targets flashed for 100ms around the time of a saccade. *Vision Research*, *47*(14), 1924–1934.

Jonides, J., Irwin, D. E., & Yantis, S. (1982). Integrating visual information from successive fixations. *Science*, *215*(4529), 192–194.

Jonides, J., Irwin, D. E., & Yantis, S. (1983). Failure to integrate information from successive fixations. *Science*, *222*(4620), 188.

Judge, S. J., Wurtz, R. H., & Richmond, B. J. (1980). Vision during saccadic eye movements. I. Visual interactions in striate cortex. *Journal of Neurophysiology*, *43*(4), 1133 –1155.

Jürgens, R., & Becker, W. (2006). Perception of angular displacement without landmarks: evidence for Bayesian fusion of vestibular, optokinetic, podokinesthetic, and cognitive information. *Experimental Brain Research*, *174*(3), 528–543.

Kagan, I., Gur, M., & Snodderly, D. M. (2008). Saccades and drifts differentially modulate neuronal activity in V1: Effects of retinal image motion, position, and extraretinal influences. *Journal of Vision*, *8*(14).

Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.

Keith, G., & Crawford, J. D. (2008). Saccade-related remapping of target representations between topographic maps: a neural network study. *Journal of Computational Neuroscience*, *24*(2), 157–178.

Kennard, D. W., Hartmann, R. W., Kraft, D. P., & Boshes, B. (1970). Perceptual suppression of afterimages. *Vision Research*, *10*(7), 575–585.

Klier, E. M., & Angelaki, D. E. (2008). Spatial updating and the maintenance of visual constancy. *Neuroscience*, *156*(4), 801–818.

Klier, E. M., Angelaki, D. E., & Hess, B. J. M. (2005). Roles of Gravitational Cues and Efference Copy Signals in the Rotational Updating of Memory Saccades. *Journal of Neurophysiology*, *94*(1), 468 –478.

Klier, E. M., Angelaki, D. E., & Hess, B. J. M. (2007). Human Visuospatial Updating After Noncommutative Rotations. *Journal of Neurophysiology*, *98*(1), 537–541.

Klier, E. M., Hess, B. J. M., & Angelaki, D. E. (2006). Differences in the Accuracy of Human Visuospatial Memory After Yaw and Roll Rotations. *Journal of Neurophysiology*, *95*(4), 2692–2697.

Klier, E. M., Hess, B. J. M., & Angelaki, D. E. (2008). Human Visuospatial Updating After Passive Translations in Three-Dimensional Space. *Journal of Neurophysiology*, *99*(4), 1799–1809.

Knapen, T., Rolfs, M., & Cavanagh, P. (2009). The reference frame of the motion aftereffect is retinotopic. *Journal of Vision*, *9*(5), 1–7.

Knapen, T., Rolfs, M., Wexler, M., & Cavanagh, P. (2010). The reference frame of the tilt aftereffect. *Journal of Vision*, *10*(1), 1–13.

Koch, C., & Deubel, H. (2007). How postsaccadic visual structure affects the detection of intrasaccadic target displacements. In R. P. G. van Gompel, M. H. Fisher, W. S. Murray, & R. L. Hill (Eds.), *Eye movements: A window on mind and brain.* (pp. 193–212). Oxford,UK: Elsevier.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916.

Kusunoki, M., & Goldberg, M. E. (2003). The Time Course of Perisaccadic Receptive Field Shifts in the Lateral Intraparietal Area of the Monkey. *Journal of Neurophysiology*, *89*(3), 1519–1527.

Kusunoki, M., Gottlieb, J. P., & Goldberg, M. E. (2000). The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion, and task relevance. *Vision Research*, *40*(10-12), 1459–1468.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, *403*(6772), 892–895.

Lappe, M., Kuhlmann, S., Oerke, B., & Kaiser, M. (2006). The fate of object features during perisaccadic mislocalization. *Journal of Vision*, *6*(11).

Latour, P. L. (1962). Visual threshold during eye movements. *Vision Research*, *2*(7–8), 261–262.

Leigh, R., & Zee, D. (1999). *The Neurology of Eye Movements*. Oxford,UK: Oxford University Press.

Li, N., & Angelaki, D. E. (2005). Updating Visual Space during Motion in Depth. *Neuron*, *48*(1), 149–158.

Li, N., Wei, M., & Angelaki, D. E. (2005). Primate Memory Saccade Amplitude After Intervened Motion Depends on Target Distance. *Journal of Neurophysiology*, *94*(1), 722 –733.

Maij, F., Brenner, E., & Smeets, J. B. J. (2009). Temporal Information Can Influence Spatial Localization. *Journal of Neurophysiology*, *102*(1), 490 –495.

Maij, F., Brenner, E., & Smeets, J. B. J. (2011). Temporal Uncertainty Separates Flashes from Their Background during Saccades. *The Journal of Neuroscience*, *31*(10), 3708 –3711.

Maij, F., de Grave, D., Brenner, E., & Smeets, J. (2011). Misjudging where you felt a light switch in a dark room. *Experimental Brain Research*, *213*(2), 223–227.

Mathôt, S., & Theeuwes, J. (2010). Evidence for the predictive remapping of visual attention. *Experimental Brain Research*, *200*(1), 117–122.

Matin, E. (1974). Saccadic suppression: A review and an analysis. *Psychological Bulletin*, *81*(12), 899–917.

Matin, L., Matin, E., & Pearce, D. G. (1969). Visual perception of direction when voluntary saccades occur. I. Relation of visual direction of a fixation target extinguished before a saccade to a flash presented during the saccade. *Perception & Psychophysics*, *5*(2), 65–80.

Matin, L., Matin, E., & Pola, J. (1970). Visual perception of direction when voluntary saccades occur: II. Relation of visual direction of a fixation target extinguished before a saccade to a subsequent test flash presented before the saccade. *Perception & Psychophysics*, *8*(1), 9–14.

Matin, L., & Pearce, D. G. (1965). Visual Perception of Direction for Stimuli Flashed During Voluntary Saccadic Eye Movements. *Science*, *148*(3676), 1485–1488.

Matin, L., Picoult, E., Stevens, J. K., Edwards, M., Young, D., & MacArthur, R. (1982). Oculoparalytic illusion: visual-field dependent spatial mislocalizations by humans partially paralyzed with curare. *Science*, *216*(4542), 198 –201.

Mays, L. E., & Sparks, D. L. (1980). Saccades are spatially, not retinocentrically, coded. *Science*, *208*(4448), 1163–1165.

McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*(3), 563–581.

McConkie, G. W., & Zola, D. (1979). Is visual information integrated across successive fixations in reading? *Attention, Perception, & Psychophysics*, *25*(3), 221–224.

Medendorp, W. P. (2011). Spatial constancy mechanisms in motor control. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 476–491.

Medendorp, W. P., Goltz, H. C., & Vilis, T. (2006). Directional Selectivity of BOLD Activity in Human Posterior Parietal Cortex for Memory-Guided Double-Step Saccades. *Journal of Neurophysiology*, *95*(3), 1645 –1655.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-Centered Updating of Visual Space in Human Parietal Cortex. *The Journal of Neuroscience*, *23*(15), 6209–6214.

Medendorp, W. P., Smith, M. A., Tweed, D. B., & Crawford, J. D. (2002). Rotational Remapping in Human Spatial Memory during Eye and Head Motion. *The Journal of Neuroscience*, *22*(1), RC196.

Medendorp, W. P., Tweed, D. B., & Crawford, J. D. (2003). Motion Parallax Is Computed in the Updating of Human Spatial Memory. *The Journal of Neuroscience*, *23*(22), 8135 –8142.

Melcher, D. (2005). Spatiotopic Transfer of Visual-Form Adaptation across Saccadic Eye Movements. *Current Biology*, *15*(19), 1745–1748.

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10*(7), 903–907.

Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*(12), 466–473.

Melcher, D., & Fracasso, A. (2012). Remapping of the line motion illusion across eye movements. *Experimental Brain Research*, *218*(4), 503–514.

Melcher, D., & Morrone, M. C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nature Neuroscience*, *6*(8), 877–881.

Mergner, T., Nasios, G., & Anastasopoulos, D. (1998). Vestibular memory-contingent saccades involve somatosensory input from the body support. *NeuroReport*, *9*(7). Retrieved from http://journals.lww.com/neuroreport/Fulltext/1998/05110/Vestibular_memory_contingent_saccades_involve.41.aspx

Mergner, T., Nasios, G., Maurer, C., & Becker, W. (2001). Visual object localisation in space. Interaction of retinal, eye position, vestibular and neck proprioceptive information. *Experimental Brain Research*, *141*(1), 33–51.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial Updating in Human Parietal Cortex. *Neuron*, *39*(2), 361–373.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in Human Visual Cortex. *Journal of Neurophysiology*, *97*(2), 1738–1755.

Michels, L., & Lappe, M. (2004). Contrast dependency of saccadic compression and suppression. *Vision Research*, *44*(20), 2327–2336.

Miles, F. A. (1995). The sensing of optic flow by the primate optokinetic system. *Eye Movement Research Mechanisms, Processes, and Applications* (Vol. Volume 6, pp. 47–62). North-Holland.

Miller, J. M. (1996). Egocentric localization of a perisaccadic flash by manual pointing. *Vision Research*, *36*(6), 837–851.

Moore, T. (2006). The neurobiology of visual attention: finding sources. *Current Opinion in Neurobiology*, *16*(2), 159–165.

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373.

Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor Origins of Covert Spatial Attention. *Neuron*, *40*(4), 671–683.

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, *98*(3), 1273 –1276.

Moore, T., & Fallah, M. (2004). Microstimulation of the Frontal Eye Field and Its Effects on Covert Spatial Attention. *Journal of Neurophysiology*, *91*(1), 152 –162.

Morris, A. P., Chambers, C. D., & Mattingley, J. B. (2007). Parietal stimulation destabilizes spatial updating across saccadic eye movements. *Proceedings of the National Academy of Sciences*, *104*(21), 9069 –9074.

Morris, A. P., Kubischik, M., Hoffmann, K.-P., Krekelberg, B., & Bremmer, F. (2012). Dynamics of Eye-Position Signals in the Dorsal Visual System. *Current Biology*, *22*(3), 173–179.

Morris, A. P., Liu, C. C., Cropper, S. J., Forte, J. D., Krekelberg, B., & Mattingley, J. B. (2010). Summation of Visual Motion across Eye Movements Reflects a Nonspatial Decision Mechanism. *The Journal of Neuroscience*, *30*(29), 9821 –9830.

Morrone, M. C., Ross, J., & Burr, D. C. (1997). Apparent Position of Visual Targets during Real and Simulated Saccadic Eye Movements. *The Journal of Neuroscience*, *17*(20), 7941–7953.

Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(3), 524–529.

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(6), 4026–4031.

Neggers, S. F. W., Huijbers, W., Vrijlandt, C. M., Vlaskamp, B. N. S., Schutter, D. J. L. G., & Kenemans, J. L. (2007). TMS Pulses on the Frontal Eye Fields Break Coupling Between Visuospatial Attention and Eye Movements. *Journal of Neurophysiology*, *98*(5), 2765 –2778.

Niemeier, M., Crawford, J. D., & Tweed, D. B. (2003). Optimal transsaccadic integration explains distorted spatial perception. *Nature*, *422*(6927), 76–80.

O'Regan, J. K. (1992). Solving the "real" mysteries of visual perception: The world as an outside memory. *Canadian Journal of Psychology/Revue canadienne de psychologie*, Object perception and scene analysis, *46*(3), 461–488.

O'Regan, J. K., & Levy-Schoen, A. (1983). Integrating visual information from successive fixations:Does trans-saccadic fusion exist? *Vision Research*, *23*(8), 765–768.

O'Regan, J. K., Rensink, R. A., & Clark, J. J. (1999). Change-blindness as a result of `mudsplashes'. *Nature*, *398*(6722), 34.

Ostendorf, F., Fischer, C., Gaymard, B., & Ploner, C. J. (2006). Perisaccadic mislocalization without saccadic eye movements. *Neuroscience*, *137*(3), 737–745.

Ostendorf, F., Kilias, J., & Ploner, C. J. (2011). Theta-Burst Stimulation over Human Frontal Cortex Distorts Perceptual Stability across Eye Movements. *Cerebral Cortex*.

Parks, N. A., & Corballis, P. M. (2008). Electrophysiological correlates of presaccadic remapping in humans. *Psychophysiology*, *45*(5), 776–783.

Parks, N. A., & Corballis, P. M. (2010). Human transsaccadic visual processing: Presaccadic remapping and postsaccadic updating. *Neuropsychologia*, *48*(12), 3451–3458.

Peterburs, J., Gajda, K., Hoffmann, K.-P., Daum, I., & Bellebaum, C. (2011). Electrophysiological correlates of inter- and intrahemispheric saccade-related updating of visual space. *Behavioural Brain Research*, *216*(2), 496–504.

Pola, J. (2007). A model of the mechanism for the perceived location of a single flash and two successive flashes presented around the time of a saccade. *Vision Research*, *47*(21), 2798–2813.

Pola, J. (2011). An explanation of perisaccadic compression of visual space. *Vision Research*, *51*(4), 424–434.

Pollatsek, A., Rayner, K., & Collins, W. E. (1984). Integrating pictorial information across eye movements. *Journal of Experimental Psychology: General*, *113*(3), 426–442.

Pollatsek, A., Rayner, K., & Henderson, J. M. (1990). Role of spatial location in integration of pictorial information across saccades. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(1), 199–210.

Poulet, J. F. A., & Hedwig, B. (2003). A Corollary Discharge Mechanism Modulates Central Auditory Processing in Singing Crickets. *Journal of Neurophysiology*, *89*(3), 1528 –1540.

Poulet, J. F. A., & Hedwig, B. (2006). The Cellular Basis of a Corollary Discharge. *Science*, *311*(5760), 518–522.

Poulet, J. F. A., & Hedwig, B. (2007). New insights into corollary discharges mediated by identified neural pathways. *Trends in Neurosciences*, *30*(1), 14–21.

Quaia, C., Optican, L. M., & Goldberg, M. E. (1998). The maintenance of spatial accuracy by the perisaccadic remapping of visual receptive fields. *Neural Networks*, *11*(7-8), 1229–1240.

Ramcharan, E. j., Gnadt, J. w., & Sherman, S. m. (2001). The effects of saccadic eye movements on the activity of geniculate relay neurons in the monkey. *Visual Neuroscience*, *18*(02), 253–258.

Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*(3), 372–422.

Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To see or not to see: the need of attention to perceive changes in scenes. *Psychological Science*, *8*(5), 368–373.

Reppas, J. B., Usrey, W. M., & Reid, R. C. (2002). Saccadic Eye Movements Modulate Visual Responses in the Lateral Geniculate Nucleus. *Neuron*, *35*(5), 961–974.

Richmond, B. J., & Wurtz, R. H. (1980). Vision during saccadic eye movements. II. A corollary discharge to monkey superior colliculus. *Journal of Neurophysiology*, *43*(4), 1156 –1167.

Riggs, L. A., Merton, P. A., & Morton, H. B. (1974). Suppression of visual phosphenes during saccadic eye movements. *Vision Research*, *14*(10), 997–1011.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1), 31–40.

Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. *C. Umilta & M. Moscovitch (Eds.), Attention and performance XV* (pp. 231–265). Cambridge: MIT Press.

Robinson, D. A. (1963). A Method of Measuring Eye Movemnent Using a Scieral Search Coil in a Magnetic Field. *IEEE Trans Biomed Eng*, *10*(4), 137 –145.

Robinson, D. A. (1964). The mechanics of human saccadic eye movement. *The Journal of Physiology*, *174*(2), 245.

Robinson, D. L., & Wurtz, R. H. (1976). Use of an extraretinal signal by monkey superior colliculus neurons to distinguish real from self-induced stimulus movement. *Journal of Neurophysiology*, *39*(4), 852 –870.

Rock, I., & Ebenholtz, S. (1962). Stroboscopic movement based on change of phenomenal rather than retinal location. *The American Journal of Psychology*, *75*(2), 193–207.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*(2), 252–256.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccade. *Nature*, *386*, 598–601.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences*, *24*(2), 113–121.

Royal, D., Sáry, G., Schall, J., & Casagrande, V. (2006). Correlates of motor planning and postsaccadic fixation in the macaque monkey lateral geniculate nucleus. *Experimental Brain Research*, *168*(1), 62–75.

Saul, A. B. (2010). Effects of fixational saccades on response timing in macaque lateral geniculate nucleus. *Visual Neuroscience*, *27*(5-6), 171–181.

Schiller, P. H., & Sandell, J. H. (1983). Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Experimental Brain Research*, *49*(3), 381–392.

Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research*, *35*(16), 2347–2357.

Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly; Delays and localization errors in the visual system. *Nature Review Neuroscience*, *3*(3), 191.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*(5212), 889–893.

Sherrington, C. S. (1918). Observations on the sensual role of the proprioceptive nerve supply of the extrinsic ocular muscles. *Brain*, *41*(3-4), 332 –343.

Simons, D. J., & Rensink, R. A. (2005). Change blindness: past, present, and future. *Trends in Cognitive Sciences*, *9*(1), 16–20.

Smith, M. A., & Crawford, J. D. (2001). Implications of Ocular Kinematics for the Internal Updating of Visual Space. *Journal of Neurophysiology*, *86*(4), 2112 –2117.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, *386*(6621), 167–170.

Sogo, H., & Osaka, N. (2001). Perception of relation of stimuli locations successively flashed before saccade. *Vision Research*, *41*(7), 935–942.

Sommer, M. A., & Wurtz, R. H. (2000). Composition and Topographic Organization of Signals Sent From the Frontal Eye Field to the Superior Colliculus. *Journal of Neurophysiology*, *83*(4), 1979–2001.

Sommer, M. A., & Wurtz, R. H. (2002). A Pathway in Primate Brain for Internal Monitoring of Movements. *Science*, *296*(5572), 1480–1482.

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*(7117), 374–377.

Sparks, D. L., & Mays, L. E. (1983). Spatial localization of saccade targets. I. Compensation for stimulation-induced perturbations in eye position. *Journal of Neurophysiology*, *49*(1), 45–63.

Sperry, R. . (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of comparative and physiological psychology*, *43*(6), 482–489.

Stark, L., & Bridgeman, B. (1983). Role of corollary discharge in space constancy. *Attention, Perception, & Psychophysics*, *34*(4), 371–380.

Stevens, J. K., Emerson, R. C., Gerstein, G. L., Kallos, T., Neufeld, G. R., Nichols, C. W., & Rosenquist, A. C. (1976). Paralysis of the awake human: Visual perceptions. *Vision Research*, *16*(1), 93–97.

Szinte, M., & Cavanagh, P. (2011). Spatiotopic apparent motion reveals local variations in space constancy. *Journal of Vision*, *11*(2), 1–20.

Szinte, M., Wexler, M., & Cavanagh, P. (2012). Temporal dynamics of remapping captured by peri-saccadic continuous motion. *Journal of Vision*, *12*(7), 1–18.

Tehovnik, E. J., & Sommer, M. A. (1996). Compensatory saccades made to remembered targets following orbital displacement by electrically stimulating the dorsomedial frontal cortex or frontal eye fields of primates. *Brain Research*, *727*(1–2), 221–224.

Thiele, A., Henning, P., Kubischik, M., & Hoffmann, K.-P. (2002). Neural Mechanisms of Saccadic Suppression. *Science*, *295*(5564), 2460–2462.

Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye Movements Modulate Visual Receptive Fields of V4 Neurons. *Neuron*, *29*(3), 757–767.

Treue, S. (2003). Visual attention: the where, what, how and why of saliency. *Current Opinion in Neurobiology*, *13*(4), 428–432.

Umeno, M. M., & Goldberg, M. E. (1997). Spatial Processing in the Monkey Frontal Eye Field. I. Predictive Visual Responses. *Journal of Neurophysiology*, *78*(3), 1373–1383.

Umeno, M. M., & Goldberg, M. E. (2001). Spatial Processing in the Monkey Frontal Eye Field. II. Memory Responses. *Journal of Neurophysiology*, *86*(5), 2344–2352.

Van Der Werf, J., Jensen, O., Fries, P., & Medendorp, W. P. (2008). Gamma-Band Activity in Human Posterior Parietal Cortex Encodes the Motor Goal during Delayed Prosaccades and Antisaccades. *The Journal of Neuroscience*, *28*(34), 8397 –8405.

Van Pelt, S., Van Gisbergen, J. A. ., & Medendorp, W. P. (2005). Visuospatial Memory Computations During Whole-Body Rotations in Roll. *Journal of Neurophysiology*, *94*(2), 1432–1442.

VanRullen, R. (2004). A simple translation in cortical log-coordinates may account for the pattern of saccadic localization errors. *Biological Cybernetics*, *91*(3), 131–137.

Verfaillie, K., De Troy, A., & Van Rensbergen, J. (1994). Transsaccadic integration of biological motion. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*(3), 649–670.

Verstraten, F. A. J., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, *40*(26), 3651–3664.

Volkmann, F. C. (1986). Human visual suppression. *Vision Research*, *26*(9), 1401–1416.

von Helmholtz, H. (1867). *Handbuch der physiologischen Optik*. Leipzig: Voss.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften*, *37*, 464–476.

von Holst, E., & Mittelstaedt, H. (1971). The principle of reafference: Interactions between the central nervous system and the peripheral organs. In P. C. Dodwell (Ed.), *Perceptual processing: Stimulus equivalence and pattern recognition* (pp. 47–71). New York: Appleton.

Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology*, *73*(5), 1988–2003.

Watanabe, J., Noritake, A., Maeda, T., Tachi, S., & Nishida, S. (2005). Perisaccadic perception of continuous flickers. *Vision Research*, *45*(4), 413–430.

Wei, M., Li, N., Newlands, S. D., Dickman, J. D., & Angelaki, D. E. (2006). Deficits and Recovery in Visuospatial Memory During Head Motion After Bilateral Labyrinthine Lesion. *Journal of Neurophysiology*, *96*(3), 1676–1682.

Wenderoth, P., & Wiese, M. (2008). Retinotopic encoding of the direction aftereffect. *Vision Research*, *48*(19), 1949–1954.

Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie*, *61*, 161–165.

Wolbers, T., Hegarty, M., Buchel, C., & Loomis, J. M. (2008). Spatial updating: how the brain keeps track of changing object locations during observer motion. *Nature Neuroscience*, *11*(10), 1223–1230.

Wurtz, R. H. (1968). Visual Cortex Neurons: Response to Stimuli during Rapid Eye Movements. *Science*, *162*(3858), 1148 –1150.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089.

Wurtz, R. H., Joiner, W. M., & Berman, R. A. (2011). Neuronal mechanisms for visual stability: progress and problems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 492–503.

Wurtz, R. H., McAlonan, K., Cavanaugh, J., & Berman, R. A. (2011). Thalamic pathways for active vision. *Trends in Cognitive Sciences*, *15*(4), 177–184.

Wurtz, R. H., Sommer, M. A., Paré, M., & Ferraina, S. (2001). Signal transformations from cerebral cortex to superior colliculus for the generation of saccades. *Vision Research*, *41*(25–26), 3399–3412.

Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum.

Zuber, B. L., & Stark, L. (1966). Saccadic suppression: Elevation of visual threshold associated with saccadic eye movements. *Experimental Neurology*, *16*(1), 65–79.